On the evolution of vocal development in island chaffinch populations

Joseph Edwin John Cooper

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Abstract

The oscine songbirds learn songs with a remarkably high diversity of vocal learning strategies, and it remains uncertain how such variety has evolved. In most instances, individuals of a species learn songs similar in structure, but in isolated populations different patterns can emerge. Comparing island and continental populations therefore provide a platform to examine evolution in song learning, and typically this has been achieved through examining how their songs differ. In this thesis, I looked to utilise three alternative perspectives to this when comparing continental and Atlantic Island populations of the chaffinch family *Fringilla*. Firstly, I performed the first computational comparison of the sensorimotor phase of development in free-living individuals. Secondly, I assessed the presence of female singing in the Atlantic Islands, describing the acoustic structure of songs and assessing their behavioural function. Thirdly, I compared whether populations differ in how discriminate against precisely and less-precisely learned songs through speaker playback experiments. In utilising different perspectives, I aimed to produce a more complete understanding of how song learning can differ between continental and island populations and use this to isolate the underlying factors causing song learning to evolve.

Two major differences in song learning were uncovered in the Atlantic Islands *Fringilla*; female singing and the slowing of sensorimotor development. Slower development could be linked to a weakening of sexual selection, for which indirect evidence was obtained with islands chaffinches not discriminating against precisely learnt songs unlike continental birds. This finding also led to the development of a new potential factor behind the evolution of song; the degree to which individuals utilise memories of songs they produce to guide sensorimotor feedback. Female singing likely assists in defending territories instead, which are maintained year-round in the islands potentially due to reduced seasonality.

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List of Abbreviations

AIC Akaike Information Criteria.

ANOVA Analysis of Variance.

DTW Dynamic Time Warping Algorithm.

FF Fundemental Frequency.

IOI Inter-Onset Intervals.

LMM Linear Mixed Models.

MCMCglmm Monte Carlo Markov Chain generalised mixed model.

NMDS Nonmetric Multidimensional Scaling.

PCA principal components analysis.

SAP Sound Analysis Pro.

UPGMA Unweighted Pair Group Method with Arithmetic Mean.

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Chapter 1

General Introduction

1.1 An overview

Species-specific vocal signals are common in a broad range of animal taxa, often used during mate selection or intrasexual conflict (Beecher & Brenowitz, 2005). However, only in a few groups of species, such as humans, cetaceans, bats, elephants and birds, do we have evidence that learning is involved in the development of these vocalisations (Doupe & Kuhl, 1999; Gahr, 2000; Janik & Slater, 1997; Poole, Tyack, Stoeger-Horwath, & Watwood, 2005). By far the most speciose of the vocal learning clades, are the oscine songbirds, a sub-order of the Passeriformes (Catchpole & Slater, 2008). Over 6,000 songbird species have been identified to date (Dale, Dey, Delhey, Kempenaers, & Valcu, 2015; Odom, Hall, Riebel, Omland, & Langmore, 2014), with evidence of vocal learning found in all species studied to date. Patterns of song learning are generally similar within each species, and different between species (Catchpole & Slater, 2008; Kroodsma & Baylis, 1982). However, on islands, several populations have been found to produce different patterns of song learning to those of their continental kindred (M. C. Baker, 1994; Kroodsma et al., 1999; Kroodsma, Ingalls, Sherry, & Werner, 1987; Lachlan et al., 2013; Lynch & Baker, 1993; Morinay, Cardoso, Doutrelant, & Covas, 2013). As yet there is no clear consensus on why this is case.

All species of songbird examined thus far, learn songs by listening to others and learning to replicate these sounds over a period of vocal development (Beecher & Brenowitz, 2005; Kroodsma & Baylis, 1982). Comparative studies of song development have tended to focus on what individuals from different species learn (Nottebohm, 1969a; Tchernichovski, Mitra, Lints, & Nottebohm, 2001; Thorpe, 1954, 1958b), and have rarely compared how they learn in detail (with

(Marler & Peters, 1977, 1987) being notable exceptions). In this thesis, I will explore the evolution of song development using island populations of the chaffinch genus *Fringilla* to conduct a detailed comparative assessment. This includes a computational analysis of the process of song development, a description of the attributes of female songs in the Atlantic Islands, examiniation of the function of female song, and testing levels of discrimination for less-precisely learnt song in males.

1.2 What Is Bird Song?

1.2.1 Songs vs Calls

There are two main classes of vocalisations produced by the perching birds *Passeriformes*, calls and songs. Calls are produced by all birds studied to date, are largely monosyllabic and are often produced as a result of a particular stimulus (Marler, 2004). They include contact calls and conspecific flight calls, which are used to signal environmental cues such as food or predation threat, or to maintain cohesion in social groups (Marler, 2004). Songs on the other hand, are usually produced in very specific contexts usually concerning territorial defence or mate acquisition. Males which had been muted, had a greater number of territorial defence losses than wild-type birds, and individuals which were unmuted were better able to recover their territories (Eriksson & Wallin, 1986; Peek, 1972). Songs are also often the most elaborate vocalisation produced in a species (Konishi, 1985). In addition, songs are often given in periodic bouts, which are regularly produced from a specific set of locations and perches, utilising a particular body posture (Konishi, 1985).

1.2.2 Which birds sing?

Across the *Passeriformes*, there is substantial variation in who produces songs and when they produce them. For example, in many species, song production is restricted to particular time periods, such as the breeding season (Nice, 1941; Slagsvold, 1977). One feature that is shared amongst all species studied to date is that males produce song (Catchpole, 1987; Riebel, 2003). However, species vary in whether their females sing (Hall & Langmore, 2017; Odom et al., 2014; Riebel, 2003). Traditionally, female song was considered rare, or produced as a byproduct of elevated hormone levels (Catchpole & Slater, 1995). Increasing documentation of female song has changed this view, such that it can no longer be considered rare (Riebel, Odom, Langmore, & Hall, 2019). For a given species, the likelyhood of their species possessing female song appears to depend on a

combination of evolutionary history, and other environmental factors (Langmore, 1998; Odom et al., 2014; Odom, Omland, & Price, 2015; J. J. Price, Lanyon, & Omland, 2009; Riebel, 2003; Slater & Mann, 2004). In particular, there appears to be a prevalence of female singing species in the tropics (Odom et al., 2014; J. J. Price et al., 2009), where species tend to be understudied compared to their temperate counterparts (Slater & Mann, 2004).

Estimating the number of Oscines where females produce song has been challenging, since only 27% of species have had these details documented (Odom et al., 2014; Webb et al., 2016). It is currently estimated that in 64% of species, females sing (Webb et al., 2016).Odom et al. (2014) revealed that the taxonomic distribution of female song indicates it is ancestral to the songbird clade, and that in some lineages has been lost and re-gained multiple times (Odom et al., 2014; J. J. Price, 2015). From the perspective of understanding how elaborate vocal signalling evolves, it can be argued that analysis of female singing provides unique insights which could not be revealed in males (Riebel, Hall, & Langmore, 2005).

1.2.3 How song is structured?

Songs are typically described as possessing a hierarchical structure (Doupe & Kuhl, 1999). The smallest song unit is an element, which is defined as a continuous unbroken signal of high energy when observed on a spectrogram (Baptista, 1974; Doupe & Kuhl, 1999). Elements are combined together to produce syllables, which are defined as a unit or collection of unit of elements that are separated by periods of silence from the nearest unit (Baptista, 1974; Nottebohm & Nottebohm, 1978a). Time gaps between each syllable are often fairly consistent and can be classified as the rhythmic timing of the song. Collections of repeated syllables can be classified as a phrase, with songs made-up of a series of phrases (Figure 1.1.). Phrases may be produced in a particular order, with the predictability of this order, described as the sequential structure. Individual birds may produce a number of different song-types, constituting its song repertoire (Hinde, 1958; Thorpe, 1958b).

1.2.4 Interspecific and intraspecific differences in song

Patterns of song structure greatly vary from species to species (Catchpole & Slater, 1995). Brown thrashers *Toxostoma rufum* for example, can have repertoire sizes above 1000 songs (Boughey & Thompson, 1981), whilst zebra finches *Taieniopygia guttata* possess just 1 song-type each (Zann, 1996). In terms of the number of syllable-types used, some can be very simple, such as the single syllable songs of

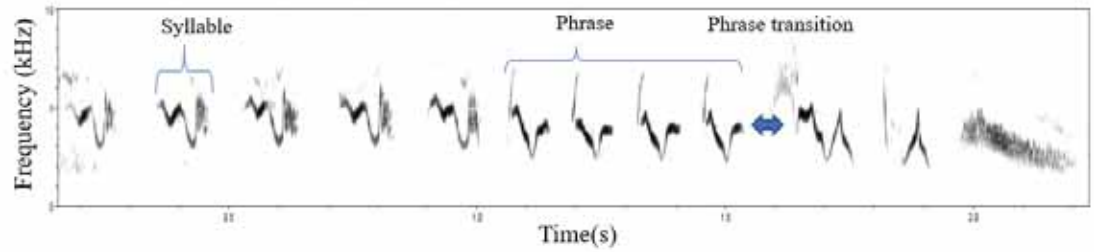


Figure 1.1: Song spectrogram of a typical adult chaffinch *Fringilla coelebs*, labelled with features of its hierarchical structure.

Henslow's sparrow *Ammodramus henslowii* (Borror & Reese, 1954) or the single repeated syllable phrase of the swamp sparrow *Melospiza georgiana* (Marler & Peters, 1977). Others, such as the skylark *Aluda arvensis* perform display flights for which song can last for over 30 minutes, where they produce producing on average 25 phrase types every 100 seconds (Briefer, Rybak, & Aubin, 2013). The syntactical structure of songs is also species specific. Chaffinches *Fringilla coelebs* imitate the sequence order of phrases produced by adults with extremely high precision (Lachlan & Slater, 2003; Thorpe, 1958a, 1958b), while the sedge warbler *Acrocephalus schoenobaenus* reproduces its repertoire of 50 or so syllables, in various combinations with each 20-second-long burst of song, rarely repeating sequences (Catchpole, 1976). In species where females sing, some such as the white-throated dipper *Cinclus cinclus* produce songs no different to those of males (Magoolagan, Mawby, Whitehead, & Sharp, 2019), whereas in other species such as the superb fairy-wren *Malurus cyaneus*, females learn songs specific for their sex (Cooney & Cockburn, 1995; Levin, 1996). Over 400 bird species from 40% of songbird families, produce duets where at their most extreme, paired bird's co-ordinate the timing and phrase-types they sing together (Hall, 2009). The number and variety of attributes a song can possess, allows for it to potentially play a key role as a prezygotic isolation mechanism (Brambilla, Janni, Guidali, & Sorace, 2008; Slabbekoorn & Smith, 2002b).

Within species, there can also be substantial geographic variation in how individuals sing (Podos & Warren, 2007). One fairly common case is for there to be patchy patterns of microgeographic variation in a song trait, with each patch recognised as a regional dialect. One of the most studied cases of this, are the dialects of the white-crowned sparrow *Zonotrichia leucophyrs nuttalli* (Baptista, 1977; Marler & Tamura, 1962). Along the coastline of the western United States, all individuals from particular areas share the same song-type, with 'sharp' boundaries separating different song-types (Baptista, 1977, 1985). The potential of dialects possessing a behaviour function has long been debated, with evidence suggesting dialects arise

as a by-product of the vocal learning process (Goodfellow & Slater, 1986; Lemon, 1975; Slater, Clements, & Goodfellow, 1984). Individuals may then adapt their responses to song to exploit this variation (Marler & Tamura, 1962; Nottebohm, 1969b; Lachlan, Janik, & Slater, 2004; Beecher & Brenowitz, 2005). In turn, this may lead to selection for song learning strategies which maximise conformity within local populations (Lachlan et al., 2004; Lachlan, Ratmann, & Nowicki, 2018).

1.2.5 Birdsong on islands

Intra-specific differences in song have also been reported when populations of a species have colonised remote islands (M. C. Baker, 1994; Hamao & Ueda, 2000; Lachlan et al., 2013; Lynch & Baker, 1993). For example, the black-capped chickadee *Poecile atricappillus* are described as 'remarkably invariant' in song across most of their range in North America, where nearly all wild individuals conform to a particular two-tone song-type (Kroodsma, Albano, Houlihan, & Wells, 1995; Kroodsma et al., 1999) . Yet in peripheral island populations, the species sings very differently, possessing a song-repertoire of at least two monotonal songs which form dialects both between and within islands (Kroodsma et al., 1999). In other cases, songs of island populations become less variable. In the North Island saddlebacks *Philesturnus refusater*, which occupy a number of islands off of New Zealand, song variability was found to be linked to the number of successive translocations that the population had experienced relative to their source (Parker, Anderson, Jenkins, & Brunton, 2012). Morinay et al. (2013) examined variation in four song traits in 49 closely related mainland and island populations. They found that individuals from the islands were less likely to include rattles and buzzes (syllables of high vibrato amplitude) and would have increased frequency bandwidth if in sympatry with fewer same-family species. Overall though, they found no consistent differences in song complexity between the mainland and islands.

Other song behaviours have also been found to be different on islands. Arcese, Stoddard, and Hiebert (1988) found that on Mandarte Island, British Columbia, female song sparrows would also produce songs unlike sparrows found in mainland North America. Similarly, in the Cocos flycatcher *Nesotriccus ridgwayi*, females initiated song bouts and produced the majority of songs on Cocos island, whereas males do so in the continental population (Kroodsma et al., 1987).

Whilst traditional island populations are separated by water, they can be separated by other unsuitable breeding habitat types such as deserts, or through

anthropomorphised segregation. For an example of the latter, consider the case of the white-backed munia *Lonchura striata*. Wild individuals of this species produce a solitary song-type, formed of a scratchy series of whistles, sung with high sequential stereotypy (Honda & Okanoya, 1999; Takahasi & Okanoya, 2010). Individuals from this species have long been domesticated, with this lighter plumaged, less-aggressive strain named the Bengalese finch or society finch *L.s.domestica*. These birds produce a highly melodic song of low sequence stereotypy, with individual syllables able to transition to multiple other syllables with every passing rendition (Clayton, 1987). Through comparing the two strains together, complex songs were preferred by females, with this complexity linked to the domestication process and domesticated environments (Honda & Okanoya, 1999).

The factors which result in song learning changes within some island populations remains unclear. Islands are typically characterised by their discrete size, low species diversity, increased population densities, reduced predation and parasitism rates, milder climate and reduced habitat variability (Losos & Ricklefs, 2009; MacArthur, Diamond, & Karr, 1972; Whittaker & Fernández-Palacios, 2007). One factor which might result in changes in song learning, is that as a result of these characteristics, island environments are more likely to carry populations of lower genetic diversity than those on the mainland (Grant, 1998). It has been argued that this could reduce the intensity of sexual selection (Griffith, Stewart, Dawson, Owens, & Burke, 1999), which in turn affects elaborate sexually selected traits, such as birdsong. An alternative mechanism which may affect song learning on islands are through founder effects. It is predicted that upon colonisation of an island, the colonists would only possess a subset of songs from their natal population (A. J. Baker & Jenkins, 1987; Harbison, Nelson, & Hahn, 1999; Potvin & Clegg, 2015; Thielcke, 1973). The lack of song models may result in unusual songs being developed. Colonisation may also be linked to change in song learning under the cultural trap hypothesis (Lachlan & Feldman, 2003; Lachlan & Slater, 1999). Here, under conditions of high drift, less restrictive song biases can evolve when signallers attempt to be recognised by targeted receivers, and receivers aim to identify conspecifics (Lachlan & Slater, 2003; Lachlan & Feldman, 2003; Lachlan et al., 2013).

Thus, it is clear that over a short time period, the rules within which songs for a particular species may align can be quickly broken and reset to form new patterns of learning. This process appears to be linked to a range of factors including reduced sexual selection, domestication, and/or colonisation of remote islands. Whilst the evolution of song has occurred readily in nature, the key changes in selection which result in the breaking and formation of song rules

remains unclear. Through running comparative studies of song between island and mainland populations, one can start to determine how songs evolve, and understand the conditions which cause this to occur.

1.3 Song learning and development

1.3.1 A historical overview

The idea that songbirds learnt their songs was suggested as early as 1773, in cross-fostering experiments on the linnet *Acanthis cannabina* and skylark (Barrington, 1773). The main breakthrough in understanding that songs were learnt came through the use of sound spectrographs by William Thorpe in the early 1950s. Thorpe manipulated the level of social isolation of captive birds and provided them with a tape tutor at various times, to assess how and when their songs were learnt (Thorpe, 1955, 1954, 1958b). After being raised by their parents, Thorpe (1954) captured chaffinches, and reared them with heterospecific birds, which were also exposed to wild chaffinch song from the outside. These birds developed songs similar in structure to a wild chaffinch. Chaffinches isolated from all songbird sounds after September developed songs with subtle changes to wild-type chaffinch song. Birds which were immediately isolated from other songs after capture, demonstrated the clearest differences in the songs they eventually learnt. Songs of isolate-reared birds showed little repetition, syllable stereotypy and lacked consistent end phrases (the terminal flourish). They did however produce flourish syllables on occasion, and produced songs of similar length, which reduced in frequency over time, indicating that some song features may have an innate basis. Thorpe (1954) remarked that these isolate birds were indistinguishable from each other, based upon song alone. Through these studies Thorpe was able to demonstrate a critical period of song development; a period of time post-fledging where individuals required to hear song in order to replicate its characteristics.

Thorpe also made key notes about the nature of how song is initially performed in young birds and how this ontogeny changes. In 1954, he adopted the term "subsong" from previous literature (Nicholson, 1931), which described a quiet warbling behaviour performed by young song sparrows *Melospiza melodia*. Thorpe noted that chaffinches produced something similar; a long, irregular ramble, typically performed during late winter and early Spring. Through comparing these songs to more-typical chaffinch songs on a spectrogram, he noted that subsong included syllables performed at extreme frequencies of a chaffinch's usual range (Thorpe, 1958b), but that these abnormal sounds would gradually be removed

over time. Given that subsong in the wild is quiet, appeared to have little territorial function (Thorpe, 1955), and was readily performed by young males when approaching new territories (Marler, 1956a), it was concluded that subsong must be part of a process of vocal development within chaffinches. In later reviews, Thorpe inferred that subsong, appeared to some degree practise for full song and could be used to study differences in song learning ability (Thorpe, 1958b).

Once the chaffinches had learnt a song, Thorpe (1954) also documented that birds would no longer be able to learn new songs, even if presented with other song stimuli. This period was coined "crystallisation" (Thorpe, 1961). Songbird species can vary whether they encounter a crystallisation period or not. Species such as the starling *Sturnus vulgaris*, continue to modify their song throughout their life and are referred to as open-ended learners (Eens, Pinxten, & Verheyen, 1992; Mountjoy & Lemon, 1995; Nottebohm & Nottebohm, 1978a). Songbirds with a brief learning window, such as the chaffinch are referred to as closed-ended learners (Beecher & Brenowitz, 2005; Eriksson & Wallin, 1986).

Marler (1956c) also coined other types of song heard in development. One was incomplete song, and usually consisted of the dropping of the flourish phrase. This was attributed to incomplete gonadal development or reduced motivation to sing and was a more common occurrence in early Spring than later in the breeding season. He also coined congested song; songs produced in a rapid sequence often alongside subsong. This hasn't been as readily adopted in the literature. Thorpe (1958b) was largely dismissive of the function of another type of song coined by his then assistant Marler, the "so-called" plastic song. Plastic song, describes a period of variability in song components and structure performed by young birds as they pass through vocal learning. Marler (1956c) noted that females would respond to plastic song in a similar manner to that of regular song.

Fernando Nottebohm took the understanding of the importance of plastic song in a new direction by incorporating ideas from Konrad Lorenz's 'innate schoolmarm', a presence that guides an organism when socially learning species-specific behaviour (Nottebohm, 1968). He examined the impact of removing auditory feedback from a bird through deafening chaffinches at select points during their life (Nottebohm, 1967, 1968). Adult birds who had developed song were uninhibited in their ability to produce them, though tended to produce incomplete songs, possibly due to a lack of motivation in a world without song. Birds deafened during the "plastic phase" of song development, could produce some features of crystallised song, but had sections which were inconsistent. Nottebohm (1968) noted the identity of phrases had begun "breaking down". No bird deafened before crystallisation,

could subsequently crystallise their song.

He also undertook an experiment to assess the factors determining how the critical period of song development occurs in chaffinches (Nottebohm, 1969a). He castrated a young chaffinch throughout its first Spring, and the bird subsequently failed to demonstrate phenotypic traits of maturity. The following year, the bird was injected with testosterone and began to display the similar characteristics of song development again, indicating a link with testosterone increase, rather than age mediating crystallisation of song.

Of birds deafened during early song development, songs produced following hormone injection were described as including syllable types of equivalent acoustic complexity to normal-type birds, but lacking syllable stereotypy and a flourish (which differentiated it from the bird deafened slightly later in its development). 4 birds deafened in midwinter (before juvenile chaffinches produce songs) had normal length song-types and produced songs within a typical frequency range for chaffinches, though lacking a gradual frequency decrease. Birds deafened having just left the nest were highly reluctant to sing without hormone treatment and developed extremely simple songs with little evidence of phrasing. Thus, Nottebohm (1969a) revealed that through increasing time lengths of deprivation from hearing conspecific song, birds became increasingly worse at producing species-typical, stereotyped songs. Production of irregular songs in birds deprived of acoustic material has since been demonstrated in a number of other species (Kroodsma & Miller, 1996; Kroodsma, Miller, & Ouellet, 1982; Marler & Tamura, 1962; Searcy, Marler, & Peters, 1985).

The next major developments in the field of song development came after Peter Marler began studying swamp sparrows and song sparrows with Susan Peters in the United States. Over a series of studies (Marler & Peters, 1977, 1981, 1982, 1987, 1988), they examined the song selection choices of developing birds, through exposing them to songs in early life and recorded weekly from 90 - 400 days. They noted that syllabic structure was highly variable; the number of syllable types used per song only reduced to a species-typical level when approaching 335 days of age. More strikingly, birds produced many more song types during their plastic phase of development, than they would following crystallisation (Marler & Peters, 1981, 1982). They coined the term "overproduction" for the production of more song-types than one will use as an adult during early development. A key difference between the concepts of plastic song and overproduction is the idea that in the latter case, some of the additional songs are also the result of imitation - being more or less accurate renditions of tutors songs. Following the

overproduction of song-types, developers go through a spell of removing songs from their repertoire, in a period termed "selective attrition" (Marler & Peters, 1982). Other studies stressed the social importance of this process, with birds able to selecting particular song-types to learn depending on their environment (Todt, Hultsch, & Heike, 1979). (Nelson, 1992b) found that field sparrows *Spizella pusilla*, and white-crowned sparrows sing a number of different song-types when first settling territories, but select one to sing in later life, which best matches the song of their territorial neighbour and perform this even after the memorisation for song learning ends.

Marler and Peters (1977) also examined how predispositions for conspecific song impacted development. Swamp sparrows were presented with song models of their own species, those from the song sparrow *Melospiza melodia*, or a mix of both. They found that swamp sparrows would only learn syllables of their own species, omitting the heterospecific syllables entirely. Furthermore, if swamp sparrow syllables were presented in the more complex syntactical organisation of the song sparrow, young males would learn these songs. In a later study, Marler and Peters (1988) presented song sparrows these songs instead and found that they would learn syllables of the heterospecific swamp sparrow. This provided the first indication that closely related species had diverged in their predisposition for conspecific signals, with the song sparrow appearing to pick from a broader array of sounds than the swamp sparrow.

Overall the classic period of song development work established that songbirds learnt their songs over two broad phases; sensory and sensorimotor. In the sensory phase, young birds are sensitive to the songs of others and commit these songs to memory. Songbirds possess an innate predisposition for which songs to memorise, and the variability of these predispositions can change from species to species. In the sensorimotor phase, birds start to try and replicate what they have memorised, though songs produced initially are highly variable. Features of song produced during sensorimotor development were placed into categories, labelled subsong, plastic song and crystallised song. Within plastic song, developers may end up producing more song-types than they utilise and go through a period of attrition before they crystallise their repertoire. However, several features of song development continued to remain unanswered. How did song development result in different outcomes of song learning? Are the stages of song development clearly separable? Do birds learn all songs at the same rate, and do different birds learn the same song different ways?

1.3.2 Computing song development

In the classic period of the field described above, song development was assessed through visual assessment of spectrograms (Lynch & Baker, 1991). This method is limited in its capacity to carry out quantitative analysis of song development, or to analyse large samples of song (Krieg & Getty, 2016). Early attempts to automate song similarity consisted of cross-correlating spectrograms; sliding one song unit on top of another and measuring overlap to assess the closeness of the match (Clark, Marler, & Beeman, 1987). However, this algorithm suffered from a reliance on songs to be simple in structure, to be partitioned into simpler units first, and often provided inaccurate results (Krieg & Getty, 2016).

Tchernichovski et al. (2001) developed software, Sound Analysis Pro (SAP), which compared the average dissimilarity in song features along a linear alignment of two songs. Similarity between syllables could now be assessed over multiple acoustic features, and a 'percentage of significant similarity' index derived between pairs of songs. In tracing song development over time, sections similar to the model were compared to versions from previous days in succession, until similarity did not occur. This proved an effective method in capturing the entirety of vocal development (Tchernichovski et al., 2001), although the software was designed specifically to analyse one species: the zebra finch.

Through tracking the development of syllables in such detail, Tchernichovski et al. (2001) revealed two new developmental processes occurring in the zebra finches. The first of these was that syllables could be learnt using two strategies. In one, syllables increasingly resembled those of the tutor as the bird aged. In the other, syllables became increasingly dissimilar to that of the tutor, before a sudden correction resulted in a correct imitation. The second finding of Tchernichovski et al. (2001) was that some yearlings produced proto-syllables and repeated these regularly during the early stages of song development. Then as the individual developed, it would transform these proto-syllables in turn, into the syllables of the tutor song. Development in this style was later termed as serial repetition (Liu, Gardner, & Nottebohm, 2004), differed from "motif learning". In motif learning, young birds appeared to imitate the sequential structure of a tutor song, before they were able to precisely imitate the tutor syllables (Liu et al., 2004).

Other programs to analyse song have since been developed. Unlike Sound Analysis Pro SAP, Luscinia utilises a dynamic alignment, using a dynamic time warping algorithm (DTW) to conduct acoustic comparisons. This searches for the optimal alignment between two sounds and compares them over a number of acoustic features including time (Lachlan, Verhagen, Peters, & Cate, 2010; Lachlan,

Van Heijningen, Ter Haar, & Ten Cate, 2016; Lachlan et al., 2013). This technique has already been utilised to compare newly-developed song to adult song (Holveck, Vieira de Castro, Lachlan, ten Cate, & Riebel, 2008) as well as comparing change in syntactical structure in a colonisation chain of related songbird populations (Lachlan et al., 2013).

The computational era of song analysis has allowed us to examine song development in a more quantitative manner than previously, allowing for greater samples of songs to be analysed. It has revealed that songs can develop using a number of strategies, and that the same song-type can be learnt using different strategies in different birds. Until now, song development has only been assessed computationally in Zebra finches and Bengalese finches, partially because of the use of SAP. As a result, questions regarding how changes in song development correlate with the evolution of song learning remain unanswered. However through Luscinia, we now have the tools to produce quantitative comparisons of song development between individuals from a wide range of species.

1.3.3 Song development in the wild

The vast majority of studies concerning song development have either used individuals raised wholly in captivity, or captured wild birds when extremely young (Liu & Kroodsma, 2006; Mennill et al., 2018). Due to factors such as high rates of territory floating (Roper, pers comm), low capture rates of yearlings and limited data collection relative to captive birds, measuring song development of individuals in the field has been extremely difficult to date (Riebel, Lachlan, & Slater, 2015). This affected how song development is studied in two key ways. Firstly, the number of species which can be raised in captivity and behave naturally in these environments is limited, leading to restrictions in which birds have had their song development studied. This restricts the capacity to study the diversity an evolution of song learning. One of the main factors which promotes the use of song as model for examining social learning is the diversity of learning strategies, and restrictions on the species that can be studied mitigates this benefit. Secondly, it is very difficult to replicate the sensory and social stimuli which a wild bird would experience as it develops. In studies of social learning across animal taxa, the importance of examining behaviour in natural contexts has been recognised, to prevent key processes from being missed (Laland, 2004; Rendell et al., 2011).

Song learning has been studied in the wild indirectly, looking at the results of song development rather than at its process (Nelson, 1992a; Nelson, Marler, & Morton, 1996). For example, male chipping sparrows *Spizella passerina* were

ringed in the nest and recorded after developing their songs in newly established territories (Liu & Kroodsma, 2006). The song-type learnt was an imitation of one of their current neighbours, indicating the sensory phase of development occurred post-dispersal. A more recent approach was developed by Roper, Harmer, and Brunton (2018) who compared song development in both male and female New Zealand bellbirds *Anthornis melanura* and did so by combining song recordings across an individuals' sensorimotor phase together, comparing them to further recordings made during adulthood. These investigations lacked examinations from multiple time-points during song development, a key feature of studies of song development in captive birds (Marler & Peters, 1982; Tchernichovski et al., 2001; Thorpe, 1958b). Very recently, Mennill et al. (2018) were able to experimentally demonstrate the process of song learning in the wild for the first time, through broadcasting savannah sparrow *Passerculus sandwichensis* song from playback speakers, including those of distant, unheard dialects. Individuals were found to learn songs from these previously alien dialects, and there was also evidence that these alien song-types could then passed on to subsequent generations.

Recent studies have demonstrated the possibility of examining song development in free-living songbirds. But as yet, similar computational methods to those used by (Liu et al., 2004; Tchernichovski et al., 2001) have not been adapted to examine wild individuals. Detailed, natural examination of song development would help ascertain whether our understanding of development from measuring captive individuals is reflective of the process in nature. In addition, comparing the development of individuals which learn songs differently, would provide an opportunity to examine whether this evolution is as a result of changes in song development, and highlight what those changes can be. This could then be used to better understand the ecological, social, or evolutionary factors that could result in the evolution of song.

1.4 The Chaffinches

1.4.1 *Fringilla coelebs* in continental Europe

To assess the evolution of song and song development, I have studied the chaffinch genus *Fringilla*. One of these is the chaffinch *F.coelebs* (Figure 1.2), which has previously served as a model species for studying song learning (Kling & Stevenson-Hinde, 1977; Lachlan et al., 2013; Nottebohm, 1968; Riebel et al., 2015; Riebel & Slater, 1999b; Slater & Ince, 1979; Thorpe, 1954, 1958b). It is common across the majority of the Western Palearctic, and easy to locate in the field (del Hoyo,

Elliott, & Christie, 2011; Marler, 1956a; Newton, 1964) . Males are territorial and regularly sing from the same position within a tree or atop a hedgerow (Marler, 1956b, 1956a; Newton, 1964). Male chaffinches have a song repertoire of between 1 and 6 song-types and usually repeat one song-type a few times before switching to another song-type in the repertoire (Marler, 1956c; Riebel & Slater, 1999b; Slater, 1981). Descriptions of song structure vary (Slater & Ince, 1979), though songs usually begin with a trill (repeated syllable phrases) and end with unrepeated phrases and a terminal flourish (see Fig. 1.1.). This syntax is strictly maintained across their continental range (Lachlan et al., 2013; Slater & Ince, 1979). Female chaffinches are not thought to sing in the wild (Kling & Stevenson-Hinde, 1977), with the behaviour having only been reported anecdotally (Halliday, 1948; Lack, 1943; Warburg, 1941). Kling and Stevenson-Hinde (1977) injected female chaffinches with testosterone prior to their first breeding seasons and found that they did end up developing songs equal in structure and syntax to that of males, indicating that females both possess the capacity to memorise song-type models prior to injection, and subsequently develop them.

Figure 1.2: A singing male chaffinch of the subspecies *F.c.gengleri*

Evidence from captive individuals revealed that chaffinches are closed-ended learners (Nottebohm, 1967, 1968, 1969a; Thorpe, 1954, 1958b). They possess a split sensory phase, with one period of memorisation occurring after fledging in June-July, and another just before territory acquisition in early February (Nottebohm, 1968, 1969a; Thorpe, 1954). Adult chaffinches begin producing

song in early February, with yearlings doing so one to two weeks later (Marler, 1956a). The time taken between the initial production of subsong and a yearling crystallising full song was found to be 6-8 weeks in captive birds (Nottebohm, 1970). Chaffinches learn to develop songs extremely precisely, copying the phrases in the song and the sequence order with which those phrases are sung in (Slater & Ince, 1979; Slater, Ince, & Colgan, 1980; Thorpe, 1958a, 1958b). The rate of cultural mutation (the production of a novel song-type rather than the tutor song), was estimated at rates of around 1% Lachlan and Slater (2003).

1.4.2 *F.coelebs* in islands

The chaffinch can also be found on a number of islands. Some, such as the British Isles, Mediterranean islands and the North Atlantic islands, were colonised naturally from the mainland population. Human translocation also led to founder populations becoming established in South Africa and New Zealand (A. J. Baker & Jenkins, 1987). From the latter, at least four islands such as Chatham Island were subsequently naturally colonised in the early twentieth century (A. J. Baker & Jenkins, 1987).

At least five genetically distinct subspecies of *F.coelebs* are distributed across the various islands in the North Atlantic (A. J. Baker, Dennison, Lynch, & Le Grand, 1990; Delgado, Calabuig, Suárez, Trujillo, & Suárez-Rancel, 2016; Illera et al., 2018; Lifjeld et al., 2016). Garcia-del Rey (2018) estimated colonisation of these islands occurred at least 0.5 mya, whereas the majority of the European continental birds would have recolonised the continent much more recently, c. 20,000-50,000 ya following the last glacial maximum (Griswold & Baker, 2002), from Northern Africa. Examination of mitochondrial DNA of these subspecies has revealed that chaffinches likely colonised the Atlantic Islands in an island-hopping manner, rather than colonising each island independently (Garcia-del Rey, 2018; Lifjeld et al., 2016). The suspected route of this colonisation chain began with arrival on the Azores and was followed by Madeira and lastly the Canary Islands, where the Eastern Islands were colonised first.

On the majority of islands where they live, chaffinches learn songs in a similar manner to that of birds from continental Europe. The primary island population that has been examined is the British subspecies of chaffinch *F.c.gengleri*. Patterns of song structure in this population (Ince, Slater, & Band Weismann, 1980; Lachlan & Slater, 2003) were similar to those reported in populations of the continental subspecies *F.c.coelebs* (Conrads, 1977; Metzmacher, 1982). Lachlan et al. (2013) examined syntactical structure in a number of chaffinch populations.

Through the use of acoustic comparisons derived from a dynamic time warping algorithm, chaffinch phrases were divided into six categories, and the predictability of one phrase category following another assessed. High phrase category transition predictability would be indicative of high syntactical structure within the population. Again, only very minor differences were found between populations in Great Britain and those from mainland Europe. Estimates of cultural mutation, the frequency with which songs turnover in a population, were also estimated to be at similar levels between *F.c.gengleri* and *F.c.coelebs* populations (Riebel et al., 2015).

Similar patterns of song learning to continental populations were also found on smaller and more recently colonised islands. Song features were found to be consistent between chaffinches on the Orkney Islands to those recorded in southern England (Slater et al., 1984). Lachlan and Slater (2003) examined cultural mutation rates between Great Britain and those of the Hebridean and Orcadian Islands, which had been naturally founded following reforestation efforts since the eighteenth century. Whilst it was found that rates of song sharing were higher in the Scottish Islands than in the British population, rates of cultural mutation were estimated at being the same. A. J. Baker and Jenkins (1987) investigated the songs of chaffinches on Chatham Island compared with those of neighbouring New Zealand. They found that though the birds on Chatham Island had a less diverse pool of syllable types from which songs were constructed, 90% of those syllables were derived from the New Zealand population. Further analysis of song structure also indicated that these songs had not changed significantly from their source population, and thus were unaffected by founder effects of colonisation.

On the other hand, it has long been noted that the Atlantic Island populations have largely different song structure to that of other chaffinch populations (Lack & Southern, 1949; Marler & Boatman, 1951). Lynch and Baker (1993) compared the differences between the songs of continental and Atlantic Island chaffinches. Samples were collected in 17 populations, with songs classified by visual inspection of spectrograms. In terms of syllable diversity, the mainland and the Atlantic Islands were quite similar. They did find increased syllable diversity on the Azores, but attributed this to high population density as a result of a lack of natural predators and reduced heterospecific competition. When the diversity of longer phrase sequences were examined, Lynch and Baker (1993) found significantly higher diversity than those in Iberia. They inferred this was due to higher rates of song recombination, where birds would "mix and match" songs from multiple tutors together, the possession of a looser song syntax and higher variability in

inter-phrase syllable morphology. They likened these island songs to plastic song of the continental birds and considered relaxed selection pressures in a less speciose environment to be a likely cause for the discrepancy between the islands and the mainland song. Whilst this might be the case, the Lynch and Baker (1993) study does possess a number of weaknesses. Sample sizes from each population are quite low, particularly in the case of the Canary Islands. In addition, categorisation of song-types was carried out through spectrogram inspection rather than through using computational methods. Given that songs recorded were being compared for similarity between 100+ others, manual inspection would likely result in frequent errors.

Lachlan et al. (2013) also examined syntactical structure in the Atlantic Islands chaffinches. They found that the islands had lower syntactical structure compared to the mainland, and that the degree of this reduction followed the suspected island-hopping colonisation path closely. Given these findings, they suggested that a temporary reduction in available song models, such as those which occur following colonisation, might impact both male song acquisition and female song selection, which could lead to unusual song learning biases.

1.4.3 *Fringilla teydea*

Another two members of *Fringillidae* are endemic to the Atlantic Islands. The blue chaffinches, were recently split into two species, found on Gran Canaria, *Fringilla polatzeki*, and Tenerife, *Fringilla teydea*, respectively (Lifjeld et al., 2016; Sangster, Rodríguez-Godoy, Roselaar, Robb, & Luksenburg, 2016). The Tenerife blue chaffinch was found to be most closely related to *spodiogenys* subspecies of chaffinch which resides in Northern Africa (Rando, Alcover, & Illera, 2010). Comparative assessment of mtDNA indicates that they shared a common ancestor roughly 2mya (Rando et al., 2010). The Gran Canaria blue chaffinch is critically endangered (Sangster et al., 2016), whilst the Tenerife blue chaffinch is fairly common in Tenerife. The latter is found exclusively in the high altitude Canarian Pine forest, and there is some overlap between their habitat and that occupied by *F.c.canariensis* (Slater & Catchpole, 1990). A playback experiment comparing conspecific and heterospecific song in these both Tenerife chaffinch species found a much stronger response for conspecific song (Slater & Catchpole, 1990). Later, Lynch and Baker (1991) found that responses to heterospecific song were much greater in individuals living in sympatry.

In terms of the structure of the song, male song is considered to be simpler than that of *F.c.gengleri*, consisting of a set of repeated syllables and then several

buzzy syllables (Lifjeld et al., 2016). Most individuals possess a repertoire of a single song-type, though occasionally individuals have two (Lifjeld et al., 2016). Regarding song development, little is known about the species, though analysis of singing adults has revealed high precision learning of song-types, and high rates of neighbour song sharing (Lachlan, in prep). It can therefore be considered that some aspects of song learning are more similar to *F.c.gengleri* (whole-song type learning), and others which might be considered more similar to *F.c.canariensis* (reduced song complexity, high rates of neighbour song sharing). Female song has not been reported (Garamszegi, Pavlova, Eens, & Møller, 2007).

1.4.4 Evolution of song in the Atlantic Islands chaffinches

It is evident that the patterns of song learning that have arisen in the chaffinches of the Atlantic Islands represent an evolution on those from their natal population. In *F.coelebs*, individuals in the islands no longer learn song-types precisely (Lynch & Baker, 1993), and as populations they have less structure in how they sequence acoustically similar phrases (Lachlan et al., 2013). *F.teydea* have a smaller song repertoire and produce songs with less phrases than *F.coelebs*, but have retained the high degree of song learning precision of continental *F.coelebs*. Therefore overall, the chaffinch family can be considered a useful study system in which to examine the evolution of song. One area in which this could occur is in the process of song development, and whether different populations also develop songs differently.This could help understand the links between changes and development and the attributes of songs learnt, and help uncover the mechanisms driving the great diversity of vocal learning strategies exhibited in the songbird.

How these changes in song learning have affected the function of song have also remained unclear. In *F.coelebs*, the island populations appear to learn less precisely (Lynch and Baker (1993); Lachlan, in prep), but as yet there is no evidence on whether this has an effect on its function as a territorial or mating signal. In addition, underlying factors which resulted in changes in song function may have promoted changes to other behaviours. For example, if song learning change arose from reduced seasonality, other changes associated with this environment, such as female singing rates and annual territorial ownership may also be occurring. Such behaviours have not yet been examined in the island chaffinches.

1.5 Thesis Outline

The songs of songbirds are an example of extremely high diversity in a vocally learnt behaviour, yet it remains unclear how this diversity has evolved (Kroodsma,

2004; Beecher & Brenowitz, 2005; Mason, Pasch, Burns, & Derryberry, 2017). Typically, songbird species conform in how they learn to sing, though in isolated populations, different patterns have been found to emerge. Comparing continental and island populations provides a platform to examine evolutionary changes in patterns of song learning.

Typically, variance in song learning has been compared through examining what songbirds learn differently. As an example, in the case of the chaffinch *Fringilla coelebs*, the Atlantic Islands populations have been noted as learning songs less precisely (Lynch & Baker, 1993) and with more variable syntactical structure (Lachlan et al., 2013). However other approaches to tackling these questions, such as comparing how different bird populations learn, or the functional consequences of song differences are much more rare (Beecher, 2008). Therefore in this thesis, using the chaffinch genus *Fringilla* as a study system, I aim to better understand the diversity of song learning through apporaching the topic with the following three perspectives:

1. How does song development evolve?

2. What is the form and function of female song in a species where only males sing across the majority of its range?

3. Does the degree in which birds discriminate against less precisely learnt songs correlate to the precision in which they learn song?

By answering these questions, I aim to provide a more complete picture of how song and song learning has evolved, and in doing so, isolate the factors that resulted in song learning changes.

Tchernichovski et al. (2001) demonstrated that detailed computational assessment of the development of individual birds could reveal new insights into how songs are learnt, but as yet these methods have been extremely limited in which species have been examined (Tchernichovski et al., 2001; Lipkind et al., 2013). As a result, there remain many outstanding questions about how songs develop, particularly in relation to species with different learning characteristics to the limited species studied already, such as such as high syntactical precision and song repertoires. If methods were developed such that they could be readily applied to free-living populations, then species which possess these characteristics could be examined. Moreover, if one wished to examine the evolution of these characteristics, then related populations which differ in their possession of them could be compared in how they develop differently.

Hence, in Chapter 2 of this thesis, I demonstrate methods to examine song development in wild birds for the first time. These are utilised to answer five outstanding questions regarding the song development process, through measuring change in songs produced by the common chaffinch subspecies F.c.gengleri; which has comparable learning precision to continental chaffinches. To examine the evolution of song development, in Chapter 3 I compare the development of *F.c.gengleri* to two further populations found on Tenerife in the Atlantic Islands. The first was *F.c.canariensis*, which learns songs less precisely (Lynch & Baker, 1993), and as a population have little syntactical structure (Lachlan et al., 2013) than *F.c.gengleri*. The second was *F.teydea*, a more distantly related species to the other populations (Rando et al., 2010), which learns songs of low phrase diversity compared to *F.coelebs* but learns as precisely as continental chaffinches (Lachlan, in prep).

A previously undescribed singing behaviour present in the Atlantic Islands *Fringilla* is detailed in Chapter 4. Female *F.coelebs* and *F.teydea* are reported here as regular producers of song on the Atlantic Islands. I describe these songs and use bioacoustics analyses to compare the similarity of song between the sexes, neighbouring females and within mated pairs. In *F.coelebs*, I examine the presence of this behaviour in multiple islands, whilst in *F.teydea* I explore the relationship between the timing of female and male song. I also assess the function of this behaviour in both species through measuring responses of wild birds to speaker playback of female songs. One of the possible functions of this behaviour is for territorial defence, and this might operate as a provision for weaker territorial defence provided by male song. It is thought that selection acting against less precisely learnt songs maintains high learning precision in continental and British *F.coelebs* (Riebel et al., 2015). If this were the case, discrimination might be reduced on the Atlantic Islands, resulting in songs being learnt less precisely. In Chapter 5, I ascertain whether this is the case through running a comparative playback study on 3 subspecies of chaffinch. One was from continental Europe *F.c.coelebs* and the remaining two from the Atlantic Islands *F.c.moreletti* and *F.c.canariensis*.

In my discussion, Chapter 6, I review the relatedness between the findings of my previous chapters, in the light of previously identified differences in the populations. In particular, I focus on which factors contributed to the evolution of differences found in Chapter 3 and Chapter 4. In addition, I produce a new potential framework for how song may evolve, derived from changes in how song develops.

Chapter 2

The process of song development in the chaffinch, as studied in wild individuals

Abstract

Laboratory studies of vocal development in songbirds have uncovered that birds utilise a two-stage process, where they first memorise songs of surrounding older birds, and use these memories to guide their own vocal production through auditory feedback. Evidence of developmental change throughout this latter sensorimotor stage is currently lacking in wild birds. Here, I present the first extensive computational examination of song development in the wild, by recording 7 chaffinches (*Fringilla coelebs*) systematically throughout their sensorimotor phase of song development. Songs were compared using a dynamic time warping algorithm and the stereotypy of phrase sequencing calculated using a threshold-based match-less entropy measure. Yearling chaffinches were found taking up territories in mid-late February, at which time they produced unstructured subsong. Individuals gradually decreased the diversity of phrases used and at the same time increased the predictability through which they sequenced phrases; no evidence of clearly defined phases in development was observed. Three novel features of chaffinch song development were revealed by the analysis. Firstly, the degree to which a phrase was predictably found in its correct sequential position was dependant on developing time, but also the eventual position of the phrase within the song. Phrases destined for the beginning of the song, were found to appear much more frequently at other sequential positions during song development than phrases destined for the end of songs. Secondly, rhythmic timing was also found

to change during song development, with intervals between syllables becoming smaller and more consistent over the course of development. Thirdly, evidence for heterogeneity in how different songs were learned was also found, with complete versions of some song-types appearing in the repertoire of developmental birds many days in advance of other song-types. These findings highlight the potential for which song development can be recorded, analysed and be used to answer outstanding questions regarding the song development process. Together, they suggest that statistical models of learning might govern song development.

2.1 Introduction

As far as we know, all songbirds acquire their songs through vocal learning (Kroodsma & Baylis, 1982), though a few species studied in isolation have developed species-typical songs (Leitner, Nicholson, Leisler, DeVoogd, & Catchpole, 2002; Kroodsma, Houlihan, Fallon, & Wells, 1997). The initiation of learning occurs early in life, with young individuals passively listening to sounds in their environment (Konishi, 1965; Nottebohm, 1967). Some songs, typically those from the same species, which match a predisposition for a song, are stored as a template in long-term memory (Marler, 1970; Marler & Sherman, 1985; Mundinger, 1995). This period is known as the sensory phrase (Marler, 1970; Thorpe, 1958b) and occurs before the second period, the sensorimotor phase, though in some species these can overlap (Brainard & Doupe, 2002). In the sensorimotor phase, young birds guide their own vocal production by matching their songs to the stored song template based upon auditory feedback (Konishi, 1965; Nottebohm, 1968, 1969a, 1972b). The beginning of the sensorimotor phase is characterised by soft, highly variable songs, known as "subsong" (Marler, 1956c; Thorpe, 1955, 1954). Over time songs gradually increase in structure, such that they resemble those produced by adults, though are not produced with the same consistency (Marler & Tamura, 1962; Nottebohm, 1970; Thorpe, 1958b). This period is referred to as "plastic song" (Nottebohm, 1969a, 1970). During plastic song, individuals from some species have been shown to overproduce songs, producing more song types than they retain in their adult repertoire (Marler & Peters, 1982; Nelson, 1992a, 2000). They then go through a spell of selective attrition during which their repertoire is gradually reduced (Marler & Peters, 1982). In many species, after a period of some weeks, song production becomes very stereotyped, and their repertoire is then fixed for the remainder of their lives (Marler, 1956c, 1970; Nottebohm, 1970). This is known as song crystallisation (Konishi, 1964). Examination of the song development process has greatly improved our understanding of neural, social and evolutionary aspects of vocal learning, with the behaviour believed to share

many parallels with human language acquisition (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Brainard & Doupe, 2002, 2013; Jarvis, 2004; Marler, 1970; Marler & Peters, 1982; Nottebohm, 1972b, 2005; Tchernichovski, Lints, Derégnaucourt, Cimenser, & Mitra, 2004; Tchernichovski et al., 2001).

One of these parallels is the presence of a hierarchical structure (Berwick et al., 2011; Doupe & Kuhl, 1999; Baptista, 1974). The smallest of these units for humans, is the phoneme, which infants first acquire to form their initial syllables and words (Doupe & Kuhl, 1999; Kuhl, 2004). The equivalent in songbirds is the element, defined as a continuous unbroken signal when observed on a spectrogram (Baptista, 1974; Doupe & Kuhl, 1999). Elements form syllables, and repetitive sequences of the same syllable, known as phrases or motifs (Baptista, 1974; Nottebohm & Nottebohm, 1978a). The time gaps between the onset of each syllable can be produced with precise rhythmic timing, with syllables often separated in time by periods of silence (Saar & Mitra, 2008). Songs are formed of sequences of one or more phrases, and some species also learn the sequential order of phrases (Thorpe, 1958b). A collection of multiple song-types form the song repertoire of an individual (Hinde, 1958; Thorpe, 1958b). A complete understanding of the song development process would require investigating how each of these hierarchical levels are formed.

The recent development of computational tools for comparing songs has allowed for much more detailed analyses of development, in which the large numbers of songs produced by developing birds can be compared quantitatively. Detailed song development trajectories of young zebra finches *Taeniopygia guttata* conducted by Tchernichovski et al. (2001), revealed a number of previously unfound behaviours were being performed. They found that syllable development occurred via two distinct strategies. Either, syllables would increasingly resemble an imitation of the desired tutor syllable, or increasingly become more dissimilar from a tutor syllable, before an abrupt correction. This latter case was regarded as an indirect imitation trajectory. In addition, Tchernichovski et al. (2001) observed that some juveniles would produce repeats of proto-syllables at the start of development, and only later on would the number of syllable types diversify.

Initially, it was reported that vocally developing zebra finches would learn the syllables in their songs before the syntactical structure (Böhner, 1990; Immelmann, 1969; Zann, 1996). In general, imitation precision of zebra finches is much higher for syllable types than it is for the sequencing of those syllables (Scharff & Nottebohm, 1991). However, zebra finches raised together with a solitary adult will produce a close copy of both the syllables and the temporal order of that male's song

(Immelmann, 1969; Tchernichovski, Lints, Mitra, & Nottebohm, 1999). Liu et al. (2004) revealed that zebra finches use two main strategies to learn a song-type, serial repetition and song motif. In serial repetition, juveniles would acquire one syllable-type of a tutor song and produce repeated bouts of this syllable. Then renditions of this syllable would then split in acoustic structure, with some transformed into other syllable-types present in the song. In the motif-learning strategy, young birds produce whole song-types which are globally representative of the sequential structure of the tutor song, but with syllables lacking the phonetic similarity to the tutor song. Over time, the precision through which syllables are imitated increases, to eventually result in the production of stereotyped syllables by the end of development. It was found that that the strategy was not specific to the song-type itself as yearlings which learned the same song-type, could use different strategies to learn it. Given that zebra finches have a repertoire size of 1 (Zann, 1996), it would be highly interesting to see if these song-learning strategies would be present in species which learn multiple song-types, and whether they might use both strategies to incorporate songs into their repertoire.

At the same hierarchical level as the structure of syllables, is the speed and regularity of their production. The capacity to produce syllables at a faster rhythm has been thought to serve as another signal of singer quality (Drăgănoiu, Nagle, & Kreutzer, 2002), with evidence of female swamp sparrows displaying significantly more to songs produced with a higher trill rate (Ballentine, Hyman, & Nowicki, 2004). Techniques first developed by Saar and Mitra (2008) found evidence of rhythmic structure in juvenile song of zebra finches. However, the degree to which young birds perceive, and then latterly learn songs at a particular rhythm remains unclear (Bruno, 2017). One investigation examining rhythmic development was conducted on Bengalese finches *Lonchura striata domestica* (Sasahara, Tchernichovski, Takahasi, Suzuki, & Okanoya, 2015). This species utilises branching syllable transitions, where rather than one syllable-type always following another syllable-type, multiple possible pathways of syllable transitions could be chosen on any given rendition of the song. Through measuring the time intervals between the onset of each syllable over development, it was discovered that birds would develop rhythmic timing specific to each particular branch pathway. As the Bengalese finches produced subsong with a normally distributed rhythm, this indicates that the rhythmic consistency did change over vocal development, but it would still be unclear as to whether these changes were driven by sensorimotor learning, or because of heightened physical development.

When training zebra finches to learn new syllables, Bruno (2017) found that they would be more successful in acquiring a syllable by the end of development, if it

was heard in the same rhythm as previous syllables, and if it was short enough to be produced in the pre-existing rhythm. However, further findings Bruno and Tchernichovski (2017) suggest that even isolate reared zebra finches can possess equivalent rhythmic timing of wild-type birds. For both of these species in which rhythmic development has been computationally analysed, neither acquire songs from multiple tutors, unlike the many repertoire learning species. It therefore remains unknown whether young birds would learn to match the rhythm of the tutor of their song, or whether they possess an individual rhythm for which they learn songs at. Several studies have recently called on further examination of rhythmic development (Norton & Scharff, 2016), as well as examination of rhythm in other species (Spierings & ten Cate, 2016; ten Cate, Spierings, Hubert, & Honing, 2016). Investigating this in a repertoire learning species would help provide evidence for both of these, and would also reveal the extent of cultural transmission of rhythm.

In regard to the repertoire, it might be the case that there are different payoffs to developing different songs. For example, individual song-types may possess features which are more impressive to receivers. Some songs can be more challenging to perform than others (Podos, 1996, 1997; Podos et al., 2016), as found with motor constraints on syllable repetition in some swamp sparrow *Melospiza georgiana* songs (Hoese, Podos, Boetticher, & Nowicki, 2000; Nowicki, Westneat, & Hoese, n.d.). Features that make a song more impressive might also be dependant on the social context in which they are being sung. The matching of a song-type between an individual and a territorial neighbour, has been demonstrated to induce stronger territorial responses in song sparrows *Melospiza melodia* than unshared songs (Burt, Campbell, & Beecher, 2001; Krebs, Ashcroft, & Van Orsdol, 1981), with song-type matching deemed to be a reliable early threat signal (Akçay, Tom, Campbell, & Beecher, 2013). However, song sparrows were found to respond most aggressively to stranger songs (Burt et al., 2001). Given that in many species, song development occurs alongside the acquisition of an individual's territory, there is potential for the early development of one particular song-type to be of greater benefit in these territorial interactions while others would develop more slowly. I am not aware of any studies of such heterogenous song development to date.

A related developmental behaviour in the acquisition of the song repertoire that has been observed in songbirds is overproduction and selective attrition (DeWolfe, Baptista, & Petrinovich, 1989; Hultsch, 1991; Liu et al., 2004; Marler & Peters, 1981, 1982; Nelson, 1992a, 1992b, 2000; Nordby, Campbell, & Beecher, 2007). Possible functional consequences for this behaviour include being more effective

in interacting with territorial neighbours (Nelson, 1992a), maintain local song dialects (Baptista, 1977; Nelson, 2000). The extent of the rates of overproduction and attrition appear to vary from species to species. In swamp sparrows, three quarters of songs a male sings during "plastic song" will be discarded by adulthood (Marler & Peters, 1982; Prather, Peters, Nowicki, & Mooney, 2010), whilst the figure was reported to be only around 5-8% in Nightingales *Luscinia megarhynchos* (Geberzahn & Hultsch, 2004; Hultsch, 1991). One additional consideration here is the relative precision in which discarded songs were acquired. In swamp sparrows, discarded songs could be precisely learned imitations of adults (Marler & Peters, 1982), but in nightingales these were reported as syllables of poor copy quality (Hultsch, 1991). In these cases, observations of selective attrition were either qualitative, or based upon the difference in repertoire sizes at two-time points, one of which was during vocal development. As a result, the relationship between the degree to which songs discarded during selective attrition are precisely learnt or of low copy quality remains poorly understood.

Attempting to answer some of these key questions regarding the song development process requires moving away from the traditional laboratory settings. One of the key factors underlying why birdsong features so prominently as a model for vocal learning is the variety and specificity of songs learnt by birds, with nearly every species learning songs in a different way (Kroodsma & Baylis, 1982). By being restricted to examining development in birds that can be kept in captivity, much of this variety is missed. Also, in captivity, it is very difficult to replicate the normal exposure to social and sensory stimuli a young bird would be subjected to in free-living conditions (Beecher, 2017; Hansen, 1979; McGregor, 2005; Payne & Payne, 1997; Peters, Derryberry, & Nowicki, 2012). However, examinations of song development on free-living birds has been thought to be extremely difficult (Liu & Kroodsma, 2006; Mennill et al., 2018). Only recently was the two-stage process of song development first demonstrated in wild birds, with Canadian Savannah Sparrows *Passerculus sanwichensis* learning song-types exclusively broadcast from playback speakers and passing these down through to subsequent generations (Mennill et al., 2018). In a similar vein, no computational examination of the complete sensorimotor phase has been conducted on wild birds.

2.1.1 Research Questions and Hypotheses:

Here, I present methodological and analytical techniques to examine song development in free-living chaffinches *Fringilla coelebs*, the original model species for examining song learning (Marler, 1958, 1956a; Thorpe, 1954, 1958b). Male chaffinches learn, on average, 2 to 3 song-types, which consist of 5-7 phrases

formed of syllables, which are repeated at the beginning of the song, and normally not repeated towards the end of the song. There is anecdotal evidence of selective attrition in chaffinches, with these cases confined to the removal of heterospecific song (Marler, 1958). Most importantly from the perspective of examining the learning of hierarchic structure of song, chaffinches learn extremely precisely. Mutation rates for cultural transmission of song (the percentage of songs novel to the population learnt by yearlings) are around 1%, with nearly all young individuals precisely imitating the syllables and the sequence of the syllables of their target song (Lachlan & Slater, 2003). This high level of precision allows the testing of 6 outstanding questions regarding song development which are outlined below.

1. Can individuals be identified and repeatedly recorded throughout their sensorimotor development phase in the wild?

2. How does phrase structure and sequencing change throughout sensorimotor development?

3. To what extent are phrases learnt in their correct sequential position?

4. Does rhythmic speed and consistency change during vocal development?

5. To what extent are songs learnt heterogeneously?

6. To what extent do chaffinches exhibit overproduction and selective attrition of precisely learnt song copies?

2.1.1.1 Question 1: Can individuals be identified and repeatedly recorded throughout their sensorimotor development phase in the wild?

This first question is unique in respect to it regarding constraints on the data collected, rather than analyses of the data. Attempting to answer question 2-6, would only be possible if an observer was able to identify and record a sufficient number of songs on successive time points throughout sensorimotor development from the same yearling. Evidence that the same yearling had been recorded would be calculated through combining measurements of the likelihood of individual recognition based upon their repertoire, and the likelihood of only the targeted individual sings in a given location.

2.1.1.2 Question 2: How does phrase structure and sequencing change throughout sensorimotor development?

If song development in the wild was similar to the process observed in captive chaffinches, we would expect the beginning of song development to coincide with the production of subsong from newly territorial yearlings. It would be expected that individuals would begin development producing a large variety of different phrase types, and for these to be inconsistently sequenced. Over time the yearling would gradually produce songs which resemble those of an adult chaffinch when viewed on a spectrogram. Compared to subsong, we would expect developers to be using a smaller diversity of phrases and for these phrases to possess a moderate level of predictability. Songs produced in this period of developmental plasticity, will still possess errors relative to renditions of the song-type memorised, such as phrases placed in the incorrect place, or not all syllables within a phrase being exact copies. Over time, it would be expected that these errors would reduce, and this would correspond with a reduction in phrase diversity and increasing phrase sequencing predictability. Finally, after crystallisation, it would be expected that both the level of phrase sequencing predictability and phrase diversity would remain constant.

An alternative hypothesis is that for some chaffinches to develop song in a similar vein to the serial repetition strategy observed in some Zebra finches (Liu et al., 2004). If this were to occur, it would be expected that there would be sharp decrease in phrase diversity, as production of that song-type would consist of a solitary repeated syllable phrase. This level of phrase diversity would be lower than that of adult birds, for which each song-type is usually formed of 5-7 phrases.

2.1.1.3 Question 3: To what extent are phrases learnt in their correct sequential position?

Once a yearling is able to imitate the phrases of their memorised tutor song, there are several hypotheses for the degree to which they will be positioned in the sequential position. The expectation based upon the laboratory reared chaffinches, would be that phrases would be fairly variable in sequential position during developmental plasticity (Nottebohm, 1969a, 1970; Thorpe, 1958b). Then gradually, individuals would increase how predictably phrases were sequenced correctly. An alternative hypothesis would be for phrases to be produced only in their correct sequential position. This would be the case if chaffinches followed developmental behaviours similar to either the motif learning strategy or the serial repetition strategy (Liu et al., 2004). A combined hypothesis would be for both of these to occur, depending on features of the phrase. In regard to the impact of

phrase position on how a phrase is positioned throughout development, the null hypothesis would be that position of a phrase has no significant effect on how that phrase develops its sequential positioning.

2.1.1.4 Question 4: Does rhythmic speed and consistency change during vocal development?

Here, I will examine whether a repertoire learning species undergoes rhythmic changes in vocal development for the first time. The null hypothesis for development of rhythmic speed would be that there is no decrease in the time intervals vocally developing chaffinches sequence syllables. The alternative hypothesis would be for rhythmic speed to increase (intervals between syllables becoming smaller) over time. For rhythmic consistency, the null hypothesis would be for there to be no significant change in the variance in timings of the intervals between syllables. This would be consistent with findings of rhythmic development in the zebra finch (Bruno, 2017). Alternatively, rhythmic consistency could increase over development. In this regard, we would expect time intervals between syllables to demonstrate increasing clustering tendency as found in the Bengalese finches (Sasahara et al., 2015).

2.1.1.5 Question 5: To what extent are songs learnt heterogeneously in chaffinches?

It remains unclear how birds organise developing their repertoire in relation to song-types. The null hypothesis would be that yearlings would develop all song-types they eventually crystallise at the same rate, with song-types resembling those they eventually crystallise appearing in their repertoire at the same time-point in development. Alternatively, songs could be learnt at different time intervals, with song-types appearing in a developing birds' repertoire earlier in time than others.

2.1.1.6 Question 6: To what degree do chaffinches exhibit overproduction and selective attrition of precisely learnt song copies?

To begin tackling questions regarding overproduction and selective attrition in chaffinches, the prevalence of this behaviour first needs to be ascertained. The null hypothesis for question 6, is that chaffinches do not learn song-types which are sung by surrounding adults, which they end up not incorporating into their eventual repertoire. The alternative hypothesis is that chaffinches do exhibit overproduction and selective attrition, with the commonality of this behaviour calculated based upon the percentage of song-types which were overproduced across the yearlings.

2.2 Methods

2.2.1 Ethics

All fieldwork was conducted with permission from Queen Mary, University of London's Animal Welfare and Ethical Reveiw Board (AWERB). The capture and ringing of chaffinches were made with permission from the British Trust for Ornithology. All bird handling was performed by licenced ringers Michelle Leveque-Shaw and Samuel Crofts.

2.2.2 Field Recordings

Fieldwork was conducted in the Spring between 2015-2018 across 3 primary field sites in Great Britain, United Kingdom. The British chaffinch subspecies *F.c.gengleri* has been historically prominent in studies on the chaffinch song (Lachlan & Slater, 2003; Marler, 1956c; Nottebohm, 1968, 1969a; Thorpe, 1954, 1958b) and possesses song learning precision rates comparable with other subspecies found within continental Europe (Lachlan et al., 2013). In 2015 & 2018, Kew Gardens (51.48,-0.29) and parks in Richmond (51.44, -0.31) were surveyed, whilst in 2016 fieldwork was conducted across East Sussex, primarily in Wadhurst Park (51.06, 0.27) and Plashett Wood (50.93, 0.06). Plashett Wood had been surveyed intensively the previous year to ensure that the area was suitable for chaffinches to breed.

Each field season began in the first week of February, in accordance with prior field data regarding the onset of adult chaffinch singing (Marler, 1956a). On each, non-rainy, non-windy morning preceding the first week of February, an observer would walk on marked trails and footpaths in suitable breeding habitat between 20 mins before sunrise and 1pm. The observer would attempt to find the locations of territories being newly defended by yearling chaffinches; birds that were in the process of undergoing the sensorimotor development of their song. This was achieved through identifying singing chaffinches and recording their songs. Through audible cues and where necessary, viewing these songs on a spectrogram, yearling chaffinches could be reliably identified from older adults. Adult male chaffinch song typically comprises of 5-7 phrases, with the first 3-4 consisting of a set of repeated identical syllables. Each phrase transition is an audible switch from one syllable type to another. Adults typically possess a repertoire of between 2-3 songs and repeat these in an (AAAA..BBBBB..) pattern (Slater et al., 1980). Anecdotal evidence from earlier studies reported that yearlings were less likely to be as consitent as this (Thorpe, 1954, 1958b). To support the visual and audible

assessment of age in chaffinches, we attempted to capture territorial individuals in Warhurst Park and Plashett Wood using mist nets, to be aged in the hand. 6 individuals captured (4 adults & 2 yearlings) matched their predicted age based on the audible cues.

Following detection of a juvenile, songs were recorded with an objective of obtaining at least 40 clear song recordings. These were made using a TASCAM -DR100 and Telinga Pro-8 Twin Science Microphone held in a Telinga parabola of 570mm diameter and digitized at a sample rate of 44.1Khz onto a SanDisk USB soundcard. The co-ordinates of the recording were marked using a GPS logger (iPhone 6s, Apple) and the site re-visited on the next day. If a chaffinch producing subsong was present, then recording would commence for an additional 40+ songs. Hereafter, the site would be re-visited every 3-4 days, until the bird produced consistent "crystallised" song-types on multiple occasions. On occasions where birds were reticent to produce song, contact calls, and heterospecific male song were played from a wireless speaker (UE Boom 2, Logitech). This perceived territorial invasion, could often entice a previously silent bird to sing, or maintain a song bout for a male already producing song. In the event that an individual failed to produce 40 songs within 60-90 mins of arrival, it was then visited each subsequent day, until this total was reached. Data from a yearling was analysed if it met the following criteria; at least 300 songs recorded in at least 6 sessions.

To examine the presence of overproduction and selective attrition in yearlings, we needed to assess the songs already present in the population. Therefore, for each yearling territory we attempted to record singing adult males defending territories within 5km of the yearling. In addition, 2 adult chaffinches were also recorded over a similar period to the yearlings to provide a comparison between singing chaffinches that had already developed song.

2.2.3 Song Analysis

Recordings were processed through the package Luscinia [Version 2.17.11.22.01, rflachlan.github.io/Luscinia]. For each recording, each song was isolated through the "Add Recording" function, through manual segmentation based upon spectogram observation.

Individual song recordings were then presented as sonograms, greyscale spectrograms kept at standardised settings (256 pts window, frame rate 5ms, time step 1ms, max freq. 10,000kHz, high pass filter 1000Hz, dynamic range 40, dereverberation 100%). Each element of the song, defined as a singular unit of continuous signal, would be manually traced away from the background noise

through visual inspection. Elements were then manually grouped as syllables, such that each syllable comprised of a unit(s) of sound interspersed by silent intervals of greater than 10ms. Any syllable which appeared visually similar were grouped as a repeated syllable phrase.

For each song traced, Luscinia would measure multiple acoustic features for every time step in the spectrogram, resulting in the creation of "contours" for how each feature varied during an element. These features were time, fundamental frequency (FF), fundamental frequency (FF change), vibrato amplitude and normalised fundamental frequency (FF norm). FF change is calculated in Luscinia through an arctan transformation of the slope of the syllable (Lachlan et al., 2013). A parameter weighting of 0.02 was applied for this process. Vibrato amplitude was calculated from the difference between the maximum and minimum peaks in frequency.

The similarity of songs within a given database were then analysed through implementing a dynamic time warping algorithm (DTW hereafter) in Luscinia, a previously described method for comparing song similarity in a dataset (Lachlan et al., 2010) that has been utilised on multiple different species (Anderson, Peters, & Nowicki, 2014; Dowling, Colombelli-Négrel, & Webster, 2016), including chaffinches (Lachlan et al., 2013). This algorithm searches the optimal alignment between two sets of time series, by producing a dissimilarity matrix between each point in one time series and another, as calculated through the mean Euclidean distance of dissimilarity for the five acoustic features between each pair of points.

A weighting was applied to each acoustic feature, based upon a current best estimate of how birds discriminate against changes in sound, derived from studies of how humans perceive changes in sound (Lachlan, in press). Similar weightings have been utilised previously to compare similarity in chaffinch songs(Lachlan et al., 2013). The weightings applied were as follows: time 1, FF 0.9, FF change 0.86, vibrato amplitude 0.05, FF norm 1.26. Compression factor was set to 0.2, dividing each element into 5, and taking the average of measurements across these 5 points to generate input data for the DTW comparison. A maximum warp of 100% was utilised. Elements were stitched together within syllables, as long as the time gap between them did not exceed 30ms.

Through using a DTW in Luscinia to measure acoustic similarity, comparisons for a given database could be made at any desired level of song organisation (i.e. each element could be treated as a separate time series, or categories of elements from syllable up to each individual). In this study, comparisons at the level of phrase,

phrase transition, song and individual level were utilised, alongside a further measure, the individual-day, which shall be explained below.

In order to perform a number of analyses, individuals needed to be split into several time points across the period in which they were recorded. On a given day, the number of songs which were analysed for an individual could vary substantially, due to a range of factors including the nature of the recording environment (weather & foliage interference) and behavioural (reluctance to sing). This led to some recording days for which low sample sizes of songs were collected. If each recording day were to be taken as a separate time point, some days would be characterised by low sample sizes, leading to the potential for high error rates. To mitigate this, a separate measure, the individual-day was devised. For each individual, the number of songs recorded per day was measured. For any day (d) for which less than 30 songs were analysed, the day before and after (d $\pm$ 1) were assessed. If this total failed to rise above 30, these songs would be grouped together, and the next sequential dates were searched (d $\pm$ 2) This continued for a maximum/minimum of d $\pm$ 3. Any day (D) for which greater than 30 songs were recorded were not added to, unless <30 song sampling $\pm$ 3 days either side of it resulted in grouping as an individual-day. The date-stamp for all songs made an individual-day was set as the mean number of days since the turn of the year across all songs of that individual-day (thereby weighting the date more heavily on the day for which the most songs were analysed). DTW performed over individual-days, were calculated based upon the mean dissimilarity for all songs contained within the individual-day.

2.2.4 Question 1: Individuality

To assess the distinctiveness of individuals solely based upon acoustics, a DTW was ran on a dataset containing all songs for all developing individuals. Hierarchical clustering using Ward's Method was then performed at the individual-day level resulting in the conversion of individual-day dissimilarity scores into a dendrogram, where the Euclidian distance between two branch ends correlated to their relative acoustic dissimilarity. Smaller distances between two points equate to low dissimilarity, and larger distances equate to higher dissimilarity. A nearest neighbour algorithm was then utilised (Hwang & Wen, 1998) to compare the relationships between all individual days in a weighted bidirectional network. The position of nodes provided the optimal solution for relatedness between individual-days as calculated through measuring the 3 most related individual-days for a given individual-day, with nodes connected if they scored below a threshold value in the DTW. Through colour-coding nodes by territory, we could ascertain the

percentage of nodes connected to the same territory, with a low error rate (nodes connected between different individuals) indicative of a strong likelihood that each individual-day cluster corresponded to different individuals.

2.2.5 Question 2: Change in phrase structure and sequencing over time

The first examination of change in vocal production in relation to date, came through visual assessment of graphical representations of dissimilarity from the DTW. The first method for doing this was the production of distance matrices (Figure 2.1). Each cell represents the comparison between two units, with darker cells indicative of lower dissimilarity. Cells are ordered by time, such that comparisons of the earliest pair of units are contained in the bottom-left of the matrix, and the latest pair of units are top-right. The black diagonal represents comparisons between the unit and itself.

For an alternative graphical representation, non-metric multidimensional scaling (NMDS hereafter) plots were utilised. In these plots, each point represents a unit in the DTW, and the distance between any two units equates to their dissimilarity, as calculated through the DTW. Plots were formed from the 2 dimensions of the NMDS which demonstrated the greatest variation in the dataset. Plots could be coloured by date, to allow for visual observation of change in clustering tendency of points over time.

To analyse change in the diversity of phrases in a developing individual over time, I utilised a category-less entropy measure (Lachlan et al., 2013; Suzuki, Buck, & Tyack, 2006). Each individual was separated into sets of individual-days, Each pair of phrases per set (for example phrase A^i taken from song A, and phrase B^i taken from song B), were assessed for their dissimilarity as calculated through the DTW. If this number fell below a threshold value, the pair of phrases were classed as being of the same type, and if the dissimilarity was above the threshold value, the phrases were classed as being of a different type. The value selected, 0.075, fell below the minimum value for each individual for which any two songs were considered the same type, based upon manual classification of song-type classification from spectogram observation (mean threshold for 7 individuals 0.092, range 0.085 to 0.115).

Two sequences of phrases were then produced for each individual-day; one where each phrase was placed in its real-time chronological order, and the other where the phrases are distributed at random relative to time. Each phrase in the real

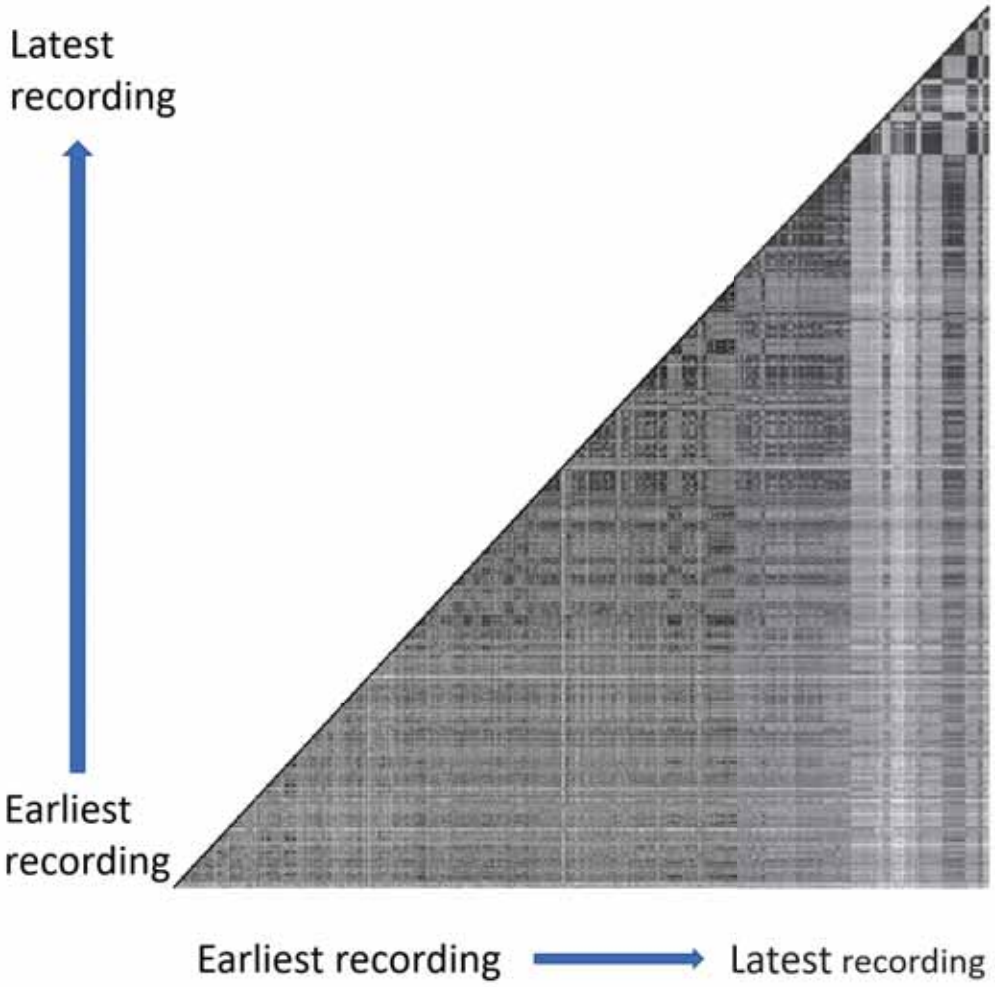


Figure 2.1: A dissimilarity matrix depicting the change in songs from a yearling through its vocal development. Each pixel in the matrix reflects an acoustic comparison between a pair of songs produced over development. The darker the pixel, the more similar the two songs are, based upon the DTW. All possible pair combinations are represented with the matrix ordered chronologically. Note that whilst songs from the earliest recordings are dissimilar to each other, later recordings alternate between dissimilar and similar songs. This reflects the AAAA..BBB.. style song bouts performed by adult chaffinches.

sequence is then compared to the phrase in its corresponding sequence in the random position. On occasions where a real phrase (A^i) belonged to the same type as the phrase in the random sequence (R^i), the subsequent phrases for each sequence were similarly assessed. This continued in turn for A^{i+n}, until the pair of phrases did not match. The number of successive phrases which did match are then averaged across phrases found in each real song (A), and the mean taken from all songs for each individual-day. This gives an estimate of phrase entropy over an individual-day. An individual would obtain a high entropy score if a large percentage of phrases were classified as being different from each other. An individual would score a low level of phrase entropy if the individual produced a high number of repeated phrases. Thus, it would be predicted that phrase entropy would decrease during song development.

To analyse change in how consistently phrases were sequenced over time, Markov-chain redundancy, ρ, was measured. This utilised match length entropy scores, as part of a ratio alongside the predictability of sequencing from the given individual-day. To calculate the latter, for a given phrase in a song (A^i) which was similar to a phrase in another song from that individual-day (B^i), the subsequent phrases in the sequences would be compared (A^{i+1} & B^{i+1}). This would continue for A^{i+n} until a pair of phrases did not match. As with the above, the score would be normalised relative to the number of phrases in the song, and then averaged across an individual-day. The value derived from the simulated data was then divided by the real data, resulting in a score between 0 and 1. This would provide an estimate for the amount of sequential structure in the dataset. A score of 0 indicated that the bird produced phrases in a completely random sequence, and a score of 1 would indicate fixed transitions. Both redundancy, ρ, and phrase entropy were then presented relative to the day of the year of the individual-day to produce individual developmental trajectories.

2.2.6 Question 3: Timing of acquiring phrases vs phrase sequences

To understand whether the relationship between the development of phrase phonetics and their sequential position, the position of each phrase needed to be attained. This was achieved by placing recordings from the last individual-day recorded into a separate DTW and producing a dissimilarity matrix for songs. This could then be displayed as a hierarchical clustering dendrogram produced using UPGMA. Through visual examination of song clusters, an observer could ascertain the shallowest depth at which 2 different song-types clustered together.

Once this threshold had been met, a song-type representative of the cluster was manually selected to be an exemplar and labelled accordingly. Hereafter, the term exemplar will refer to the songs designated in this manner.

After exemplars had been labelled for each developer, all songs from that developer were placed into another DTW. A dissimilarity matrix for phrases was produced and exported into R (Team, 2015). Each phrase was then labelled by the day of the year value of the individual-day it was assigned to, and the position within the song (the third phrase in a song would be position number 3). This system was preferred over relative phrase position, due to high rates of incomplete songs in yearling chaffinches.

For each phrase in an exemplar song (E^i), phrases (G^i) produced by the bird over the course of its development that scored less than a threshold value of dissimilarity (0.075) were identified. Pairs of phrases scoring below this value were considered to belong to the same phrase-type. Next, the phrase following the G^i (G^{n+1}) was measured for its dissimilarity with the exemplar phrase that followed E^i (E^{i+1}). These dissimilarity scores were plotted against the individual-day of the selected phrase G^i.

To ascertain whether time and position of the phrase (G^i) in the song affected the distribution of dissimilarity scores between (G^{n+1}) and (E^{i+1}), a LMM using the lme4 package in R was utilised (Bates, 2007). A series of nested models (Table 2.1) were produced, aimed at predicting the dissimilarity scores between (G^{n+1}) and (E^{i+1}) following log transformation. Individual-day date and relative phrase position as fixed effects, and exemplar song-type as a random factor. Model fit was tested through the ANOVA function in lme4 in R. The model which best explained variation in (G^{n+1}) and (E^{i+1}) dissimilarity was selected based upon scoring the lowest AIC score, as well as a log-likelihood ratio compared through a Chi-squared test.

Table 2.1: Nested models for measuring the relationship between acquiring phrases vs phrase sequences

Model	Description	
Null Model	log [dissimilarity (G^{n+1}) and (E^{i+1})]	1 +(1|exemplar)
ModelA2	log [dissimilarity (G^{n+1}) and (E^{i+1}]	date +(1|exemplar)
ModelA3	log [dissimilarity (G^{n+1}) and (E^{i+1})]	date + time +(1|exemplar)
ModelA4	log [dissimilarity (G^{n+1}) and (E^{i+1})]	date * time +(1|exemplar)

2.2.7 Question 4: The development of rhythm

To examine whether yearling chaffinches change in the consistency or speed in the time-gaps between the syllables of their songs, each syllable transition of each song from each developer was measured for the IOI (the timespan between the onset of one syllable, χ and the following syllable, χ+1). These times were then presented as phase-space plots (Ravignani, 2017), two dimensional scatter plots where the x-axis represents the IOI time between χ and χ^{+1}, and the y-axis the IOI time between χ^{+1} and χ^{+2}. Points within this scatter plot were then assessed for clustering tendency over time using the Hopkins statistic. Each syllable was time-stamped for the individual-day it was assigned and extracted into R. For each individual-day, the dissimilarity to the k-nearest neighbour of points in the scatter plot is compared to 10000 randomly generated data drawn from a normal distribution. This produces a figure of clustering tendency for each individual-day calculated through mean k nearest neighbour distance for each individual-day, divided by the mean k-nearest neighbour from both real and all simulated data-sets. The output metric is between 0.5 and 1, where randomly distributed data would score 0.5 and clustered data trending towards 1. The impact of developmental time on clustering tendency was tested through a LMM conducted using the lmer function in R (lme4). Two models were produced (Table 2.2); a null model, and one which features IOI individual-day as a fixed effect. Model fit was tested through the ANOVA function in lme4, and assessed by examining which scored the lowest AIC score, as well as if Model 2 had a significantly different log-likelihood ratio, as measured through a chi-squared test.

Table 2.2: Nested models for measuring the development of rhythm

Model	Description	
Null Model	Hopkins statistic of IOI clustering tendency	1 +(1|song)
ModelB2	Hopkins statistic of IOI clustering tendency	date + (1|song)

2.2.8 Question 5: Song learning heterogeneity

To examine whether songs are learnt simultaneously, or learnt heterogeneously, songs for each individual were placed through a separate DTW, and the dissimilarity values for the song distance matrix exported into R. Each song in the dataset was assessed for its dissimilarity with the exemplar songs from the individual. The exemplar for which it scored the lowest dissimilarity in the DTW was highlighted. Scatter plots for each individual were then produced, where the x-axis was the day of the year for the individual-day and the y-axis was the dissimilarity to the closest-match exemplar. A dissimilarity threshold was also plotted at 0.075

below which song-types would be considered to match the exemplar. Points were coloured relative to the exemplar to which it matched closest. It would be expected that if songs were learnt concurrently, that points would cluster together at all time points, and the earliest date individual colours would be represented below the lower bound of dissimilarity would occur at the same time point. If songs were learnt heterogeneously, it would be expected that some song-type matches would appear at earlier time points than others.

2.2.9 Question 6: Overproduction and Selective Attrition

To examine whether overproduction and selective attrition (defined here as the development of "real" song-types, learnt from surrounding individuals, which were discarded prior to crystallisation) was a feature of song development in chaffinches, each individual was placed in a DTW alongside a dataset of songs from adults (n= 97) recorded within 5km of 6 of the developers (not including WealdenJ2). A distance matrix of songs was produced and exported to R. Next followed a four-stage process of elimination, which would only leave potential cases of overproduced songs. Firstly, cases were removed such that pair comparisons were only being made between songs of a developer and songs of an adult (not adult v adult). Secondly, in order to locate examples of overproduction, cases needed to be located for which song-types produced by the developer matched another song type. Therefore, all pairs of songs for which the dissimilarity was 0.1 or higher were removed, as any score above this threshold would indicate songs did not match. Thirdly, for songs to be considered overproduced, they needed to not be retained in the repertoire. Therefore, any songs that were measured as having lower than 0.1 dissimilarity with the exemplar song-type for that individual were removed. For the final stage, pairs of songs which scored below 0.075 dissimilarity, were pooled and had their spectrograms manually examined. The overall level of overproduction was calculated on the number of song-types that passed this examinations compared with the total number of songs produced by yearlings.

2.3 Results

2.3.1 Recording effort and observations

In total, 7 yearlings met the criteria of having more than 300 songs recorded on at least 6 occasions (Table 2.3). 3 were located in the Richmond area (Figure 2.2d) 3 in the Sussex weald (Figure 2.2c), and 1 in Plashett Wood (Figure 2.2b). The finding of just 1 yearling in Plashett Wood was lower than had been anticipated, given that a previous population census conducted the previous summer found at

least 38 individual chaffinches holding territories in the wood. However, between Feb 1st and March 1st, only 10 individuals were detected of which 3 were new to the population, including the yearling. One additional yearling (WealdenJ3), was recorded for 171 songs, but only 12 of these were prior to crystallisation. The individual proved difficult to recover and record successfully due to both the terrain of the territory and reluctance to sing. This individual was not included in future analyses except for those concerning the individuality of developers, as these can be performed with fewer song recordings.

The majority of birds were first detected in the second to last week of February, similar to the dates reported by Marler (1956a). Following the delay in finding birds in Plashett Wood during Spring 2017, the search area for yearlings was widened on February 28th, with two additional birds located on March 1st. One of these birds was notable for being located close to a large floating flock of chaffinches which would frequently feed within the yearlings territory. These birds largely possessed different behaviour to the yearling. If the yearling detected a calling or singing chaffinch within its territory, it would readily approach and counter-sing. The flock on the other hand, were almost entirely silent, quickly flew away when approached and were unresponsive to playback. This behaviour reflects typical encounters with chaffinches which winter in the British Isles but hold their breeding territories in Scandinavia. Another observation was that yearling males were accompanied by a second male more regularly than would be expected, especially during early recording sessions. 14 out of the 50 recording sessions made in East Sussex during 2017 were noted for a second male being present, including at least one for each individual and 12 of these 14 occurring between year-day 50 and 75.

In addition to the 8 yearlings, 97 surrounding adults were recorded (n=41 in Plashett Wood with 38 recorded in Summer 2016 and 3 in Spring 2017, n=24 in Richmond, n=22 in Wealden). WealdenJ2 was recorded at a fair distance from the other territories (Table 2.3), but in the remaining birds, all but one song-type were also sung by at least 1 nearby adult. 2 adults, both in Richmond, were recorded as comparators for juvenile vocal development (Table 2.3).

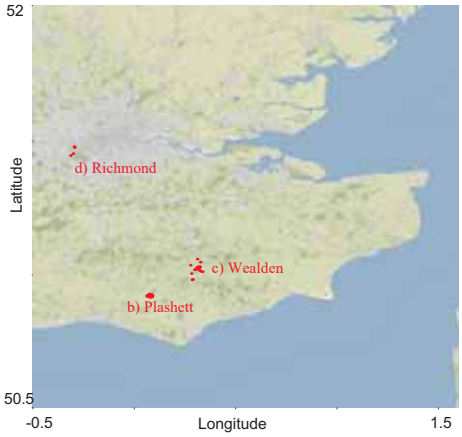
2.3.2 Question 1: Individuality, as assessed through acoustics & yearling identification

Multiple criteria were utilised to assess whether yearlings could be identified purely based upon acoustics. Firstly, as found with chaffinch populations continent-wide (Lachlan, in prep), adult chaffinches rarely shared all song-types in their repertoire.

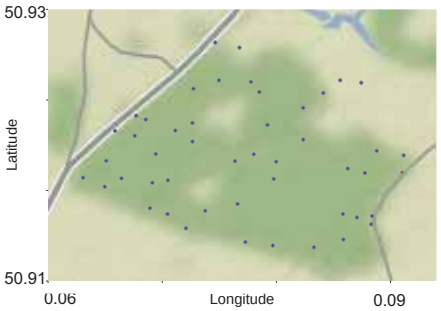
Table 2.3: Details and recording effort for yearlings and adults

Territory Latitude	Territory Longitude	Recordist	Age	Population	Name	First Recording	Last Recording	Songs Recorded	Recording Sessions
51.446	-0.312	RFL	Y	Richmond	Richmond22	17/02/2018	25/03/2018	611	12
51.479	-0.295	RFL	Y	Richmond	RichmondJ1	21/02/2015	14/04/2015	393	10
51.476	-0.292	RFL	Y	Richmond	RichmondJ2	21/02/2015	21/03/2015	375	7
51.477	-0.295	RFL	A	Richmond	RichmondA1	21/02/2015	18/04/2015	472	10
51.453	-0.300	RFL	A	Richmond	RichmondA2	21/02/2018	22/03/2018	343	8
50.921	0.091	JEJC	Y	Plashett	PlashettJ1	13/02/2017	08/04/2017	653	20
51.020	0.303	JEJC	Y	Wealden	WealdenJ1	01/03/2017	06/04/2017	328	9
50.092	0.409	JEJC	Y	Wealden	WealdenJ2	13/03/2017	06/04/2017	335	8
51.030	0.320	JEJC	Y	Wealden	WealdenJ3	01/03/2017	06/04/2017	171	5
51.024	0.320	JEJC	Y	Wealden	WealdenJ4	01/03/2017	09/04/2017	514	13

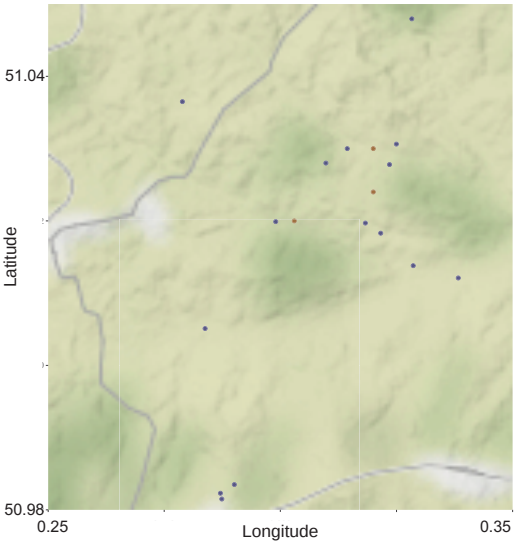
(a) South-Eastern England



(b) Plashett Wood



(c) Wadhurst Park



(d) Richmond

Figure 2.2: Co-ordinates of chaffinch territories recorded between 2015 and 2018, plotted using ggmap (Kahle & Wickham, 2013). a) The locations of each sample population in southern England, b-d) adults and yearlings recorded in b) Plashett Wood, c) Wealden Area, d) Richmond Area (2015 yearlings and 2018 individuals only). In all cases yearlings are brown points, and surrounding adults are in blue

In 42 adult birds recorded in Plashett Wood in 2016, just one pair of birds shared all of the same song-types. Secondly, all individuals (including late developmental birds for which song-types were identifiable), recorded multiple times at the same territory possessed the same song types. These two criteria combined indicate that birds did indeed sing within specific territories, and individuals recorded within those territories were highly likely to be the same individual as recorded there previously.

In regard to the acoustic analysis, when dissimilarity scores for individual-days were clustered, territories tended to cluster together (Figure 2.4). The nearest branch point for 58 of the 61 individual-days were other recordings from that territory (Figure 2.3). Importantly, these clusters were distinct even when only examining the earliest 2 recording sessions for a given territory (Figure 2.3, lowest two numbers next to the territory name). The nearest neighbour algorithm also reflected this, with the majority of individual-days clustering together (Figure 2.4), save for one putative individiaul. This individual-day was actually placed closer to recordings made in a different population, which were recorded a year later.

There was a trend for dendrogram branch depth to correlate with individual-day date, with later individual-days more closely resembling later individual-days, than earlier ones (Figure 2.3). As a result of combining both the territorial observations and the bioacoustics analysis, there is high confidence for the identification of yearlings.

2.3.3 Question 2a: Song in adult chaffinches during early Spring

Before moving on to examining song development in yearlings, I will first provide a baseline by showing how adult chaffinches change in their song consistency during early spring. The initial songs produced by the 2 adults recorded around year-day 55, shared a number of characteristics with yearling song. Phrases and phrase transitions were not produced with precise consistency, as would be expected in adults in latter parts of spring (Figure 2.5). Phrase entropy was found to be higher (Figure 2.9), and redundancy lower (Figure 2.10) than would be the case later in the year.

Whilst some qualities were similar to yearling song, other discernible features allowed these individuals to be aged successfully. Early songs produced by adults resembled song-types already in the population, in a manner that was not the

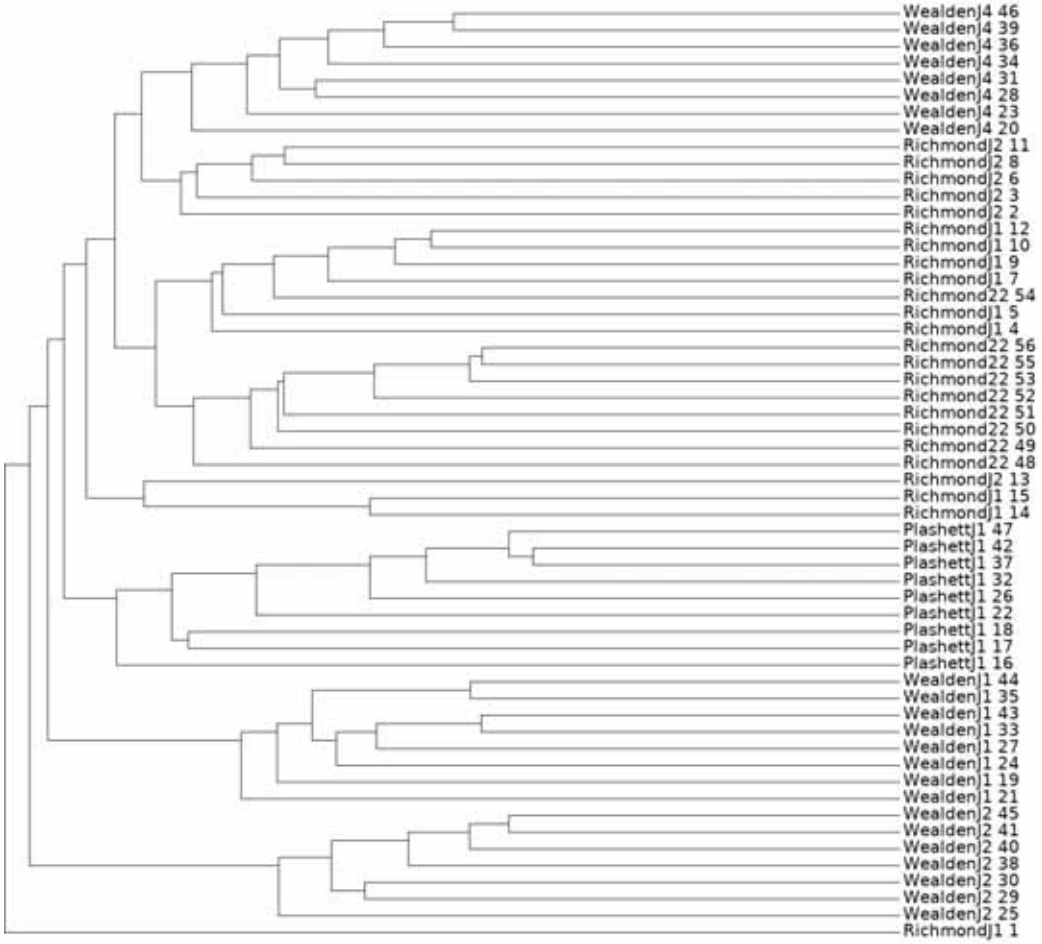


Figure 2.3: Dendrogram of individual days from the 7 yearlings. The dendrograms were calculated using Ward's Method clustering algorithm from a dissimilarity matrix generated by a DTW analysis in Luscinia. Branch names equate to the territory for which a targeted yearling bird occupies, with the number the chronological date of the individual day, with number 1 the first date the first bird was recorded.

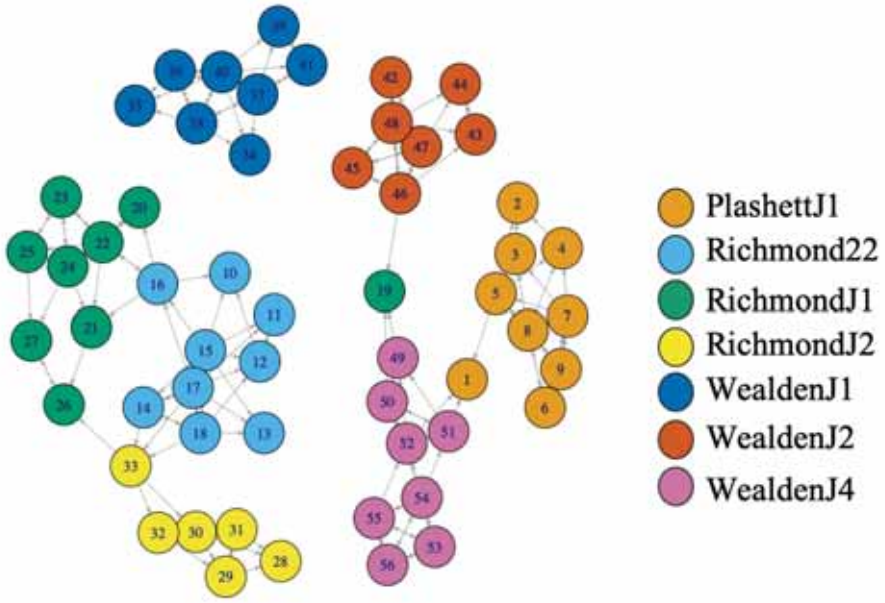


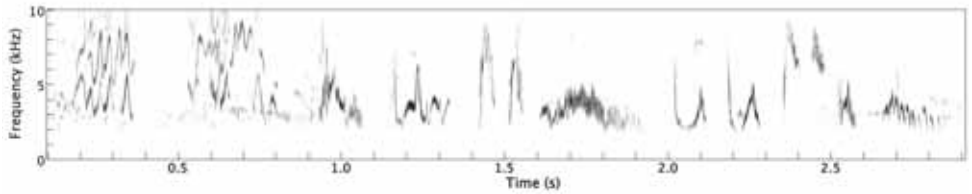
Figure 2.4: Nearest neighbour plot of individual-days for 7 yearlings. Distances between connected nodes reflects relative acoustic similarity between songs produced on different individual-days. Node clusters which fell above a required dissimilarity threshold were classed as being part of a different population (i.e. a different individual). Each individual is denoted by a starting number, and in each subsequent indiviudal-day the number increases by 1. This continues until the next individual-day when a new individual is assigned a number.

case for the first songs produced by yearlings (Figure 2.5). In addition, unlike yearling birds, adults were able to reproduce the same syllable-type multiple times in a phrase, even in the earliest recording sessions. These differences are reflected in the relative disparity between phrase entropy (Figure 2.9) and redundancy (Figure 2.10) of adults and of yearlings in the earliest recording sessions

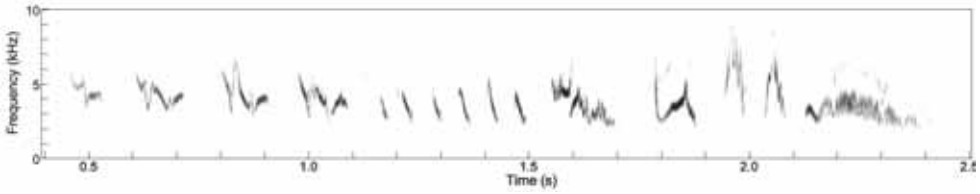
Curiously, these behaviours did not appear in all adults; in Spring 2017, only 3 of the 11 adults recorded in Spring 2017 produced songs which lacked high consistency in phrases and phrase transitions. The majority of individuals were first detected produce precise song-type imitations in highly consistent song bouts.

However, within a week of the first recording, any adult which had been recorded producing less consistent song imitations, had increased their consistency of phrase phonetics and phrase transitions to their expected high levels. Examination of NMDS plots revealed tight clusters of phrases, phrase transitions and whole-song types, at intermediate and late time points (Figure 2.6). These changes also saw a rapid rise in sequence redundancy (Figure 2.10) and sharp decrease in syllable entropy (Figure 2.9) which were maintained throughout the remaining recording period.

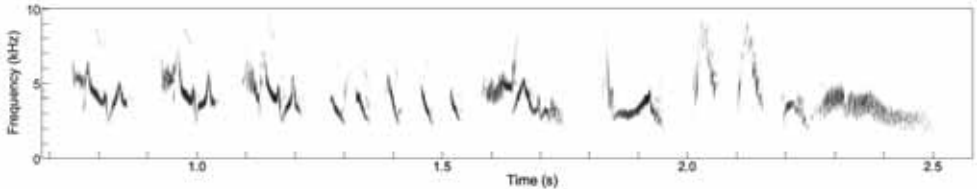
(a) 24/02



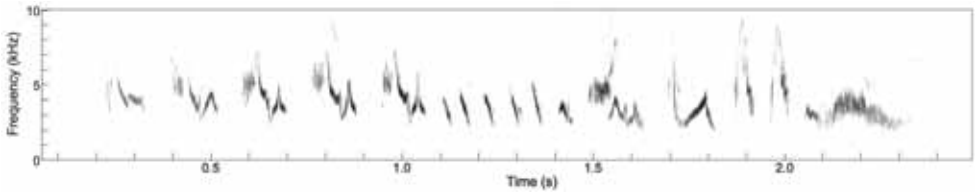
(b) 03/03



(c) 05/03



(d) 11/03



(e) 22/03

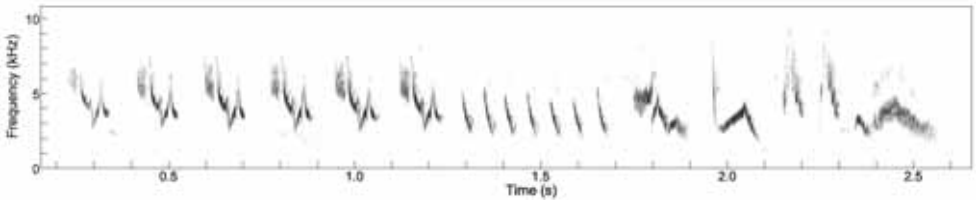


Figure 2.5: 5 representative sonograms recorded on different dates from an adult chaffinch

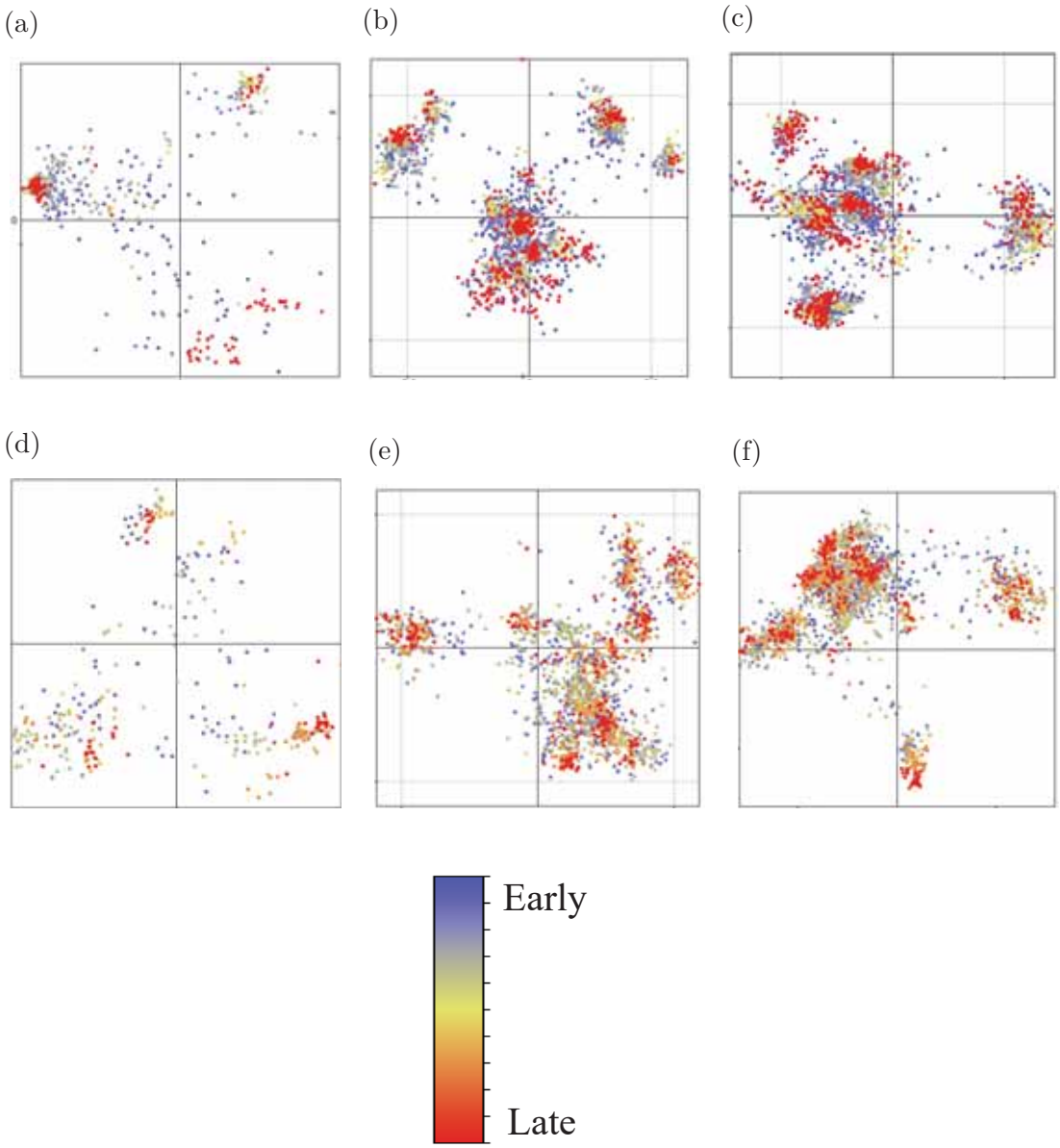


Figure 2.6: NMDS plots of change in song strucutre at 3 different levels in 3 adult chaffinches (a-c and d-f respectively). In plots a and d, each point represents songs, in plots b and e, each point represents phrases, and in plots c and f, each point represent phrase transitions. The distance between any two points reflects their acoustic similarity. Point colour is an indicator of time, with blue points being the first recorded and red the last.

2.3.4 Question 2b: Song development in yearling chaffinches

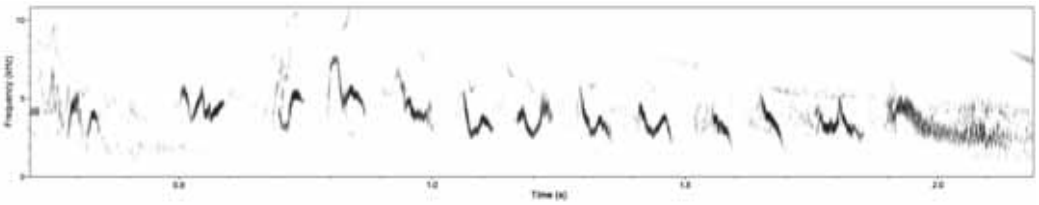
All yearlings first recorded during early to late February (year-day 32-55) possessed high phrase entropy (Figure 2.9). Songs produced by yearlings typically contained no repeated syllable-types (Figure 2.7), and songs themselves were highly variable (Figure 2.8). Phrase transitions were also highly variable, as indicated by low

levels of redundancy across all of the yearlings compared with the adults (Figure 2.10).

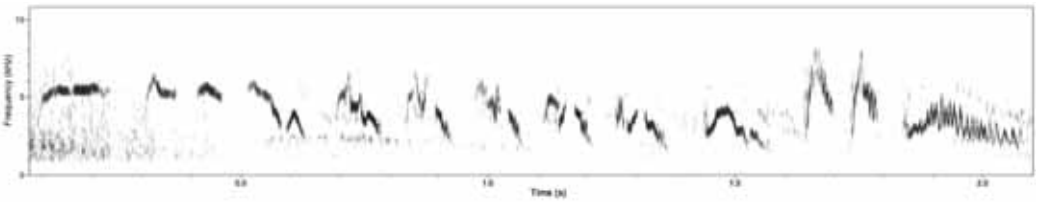
After this, a period of rapid development occurred (year-day 55-72), with yearlings reducing their level of phrase entropy, and possessing high rates of gain in sequential redundancy, comparable to that of learning rate gains in the adults, a few weeks prior (Figure 2.10). Song clusters begin to form, as song-types become distinct from one another (Figure 2.8, points coloured in grey-yellow). Whilst the rate of change in entropy, redundancy and song clustering tendency, follow a general pattern of increasing in stereotypy over time, there is considerable individual variation in the trajectories. For example, WealdenJ1 and RichmondJ1 were comparatively quicker in reducing phrase entropy than the other yearlings, with RichmondJ1 also the first to reach adult-like sequence redundancy levels. By contrast WealdenJ4 consistently had some of the lowest levels of sequence redundancy compared to other yearlings for the same time point in the year. This demonstrates, that within the general pattern of development seen within these birds, there is also substantial individual variation.

Increases in sequence redundancy and syllable entropy continued in yearlings until around day 80 of the year (Figure 2.11), by which time they had reached similar levels to that of adults (Figure 2.10). When examined on NMDS plots, song-types would clearly differentiate themselves into tight clusters by the latest recording dates, revealing repertoire sizes for the yearlings of 2 (n = 3) and 3 (n=4) song-types (Figure 2.8). The 6 individuals located within 5 miles of 20+ recorded adults, developed 16 song-types. 15 of these were precise copies song-types in the population, with 1 song-type not found in any recorded adult, though may have been present in other birds missed during surrounding recordings.

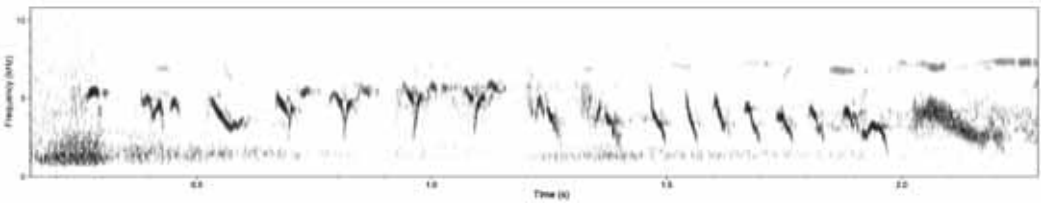
(a) 01/03



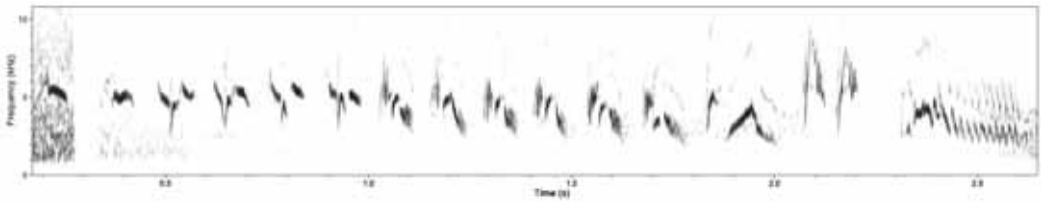
(b) 06/03



(c) 16/03



(d) 25/03



(e) 30/03

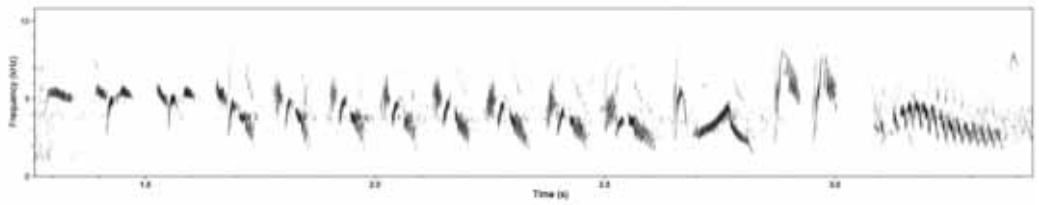


Figure 2.7: 5 representative sonograms recorded on different dates from a yearling chaffinch.

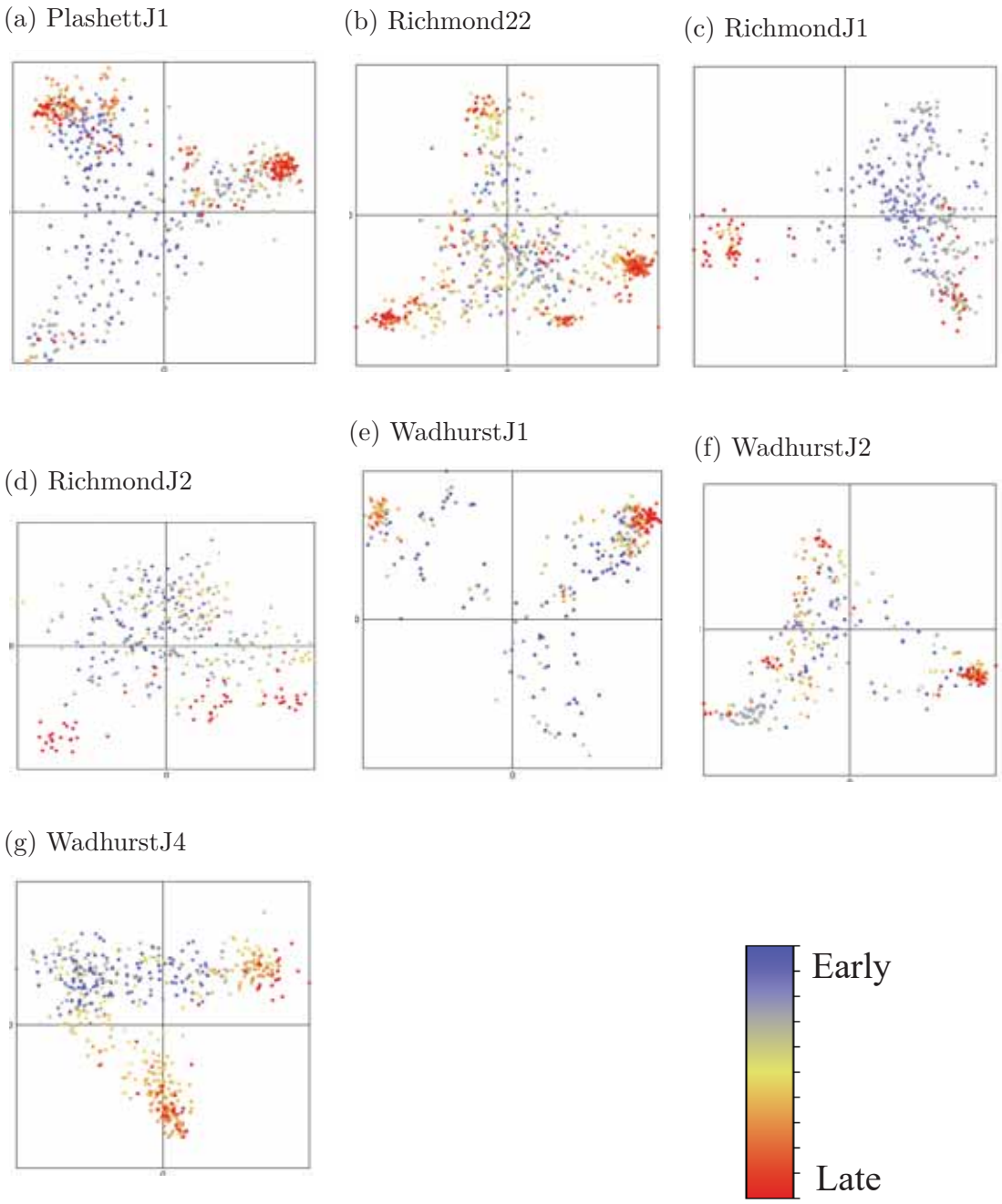


Figure 2.8: NMDS Plots for 7 yearling chaffinches, where each point represents a song, and the distance between each point equates to the dissimilarity between these two songs. Smaller distances infer greater similarity. Recording date is indicated with an individually specific colouring, with blue being the earliest recording date and red being the last recording date.

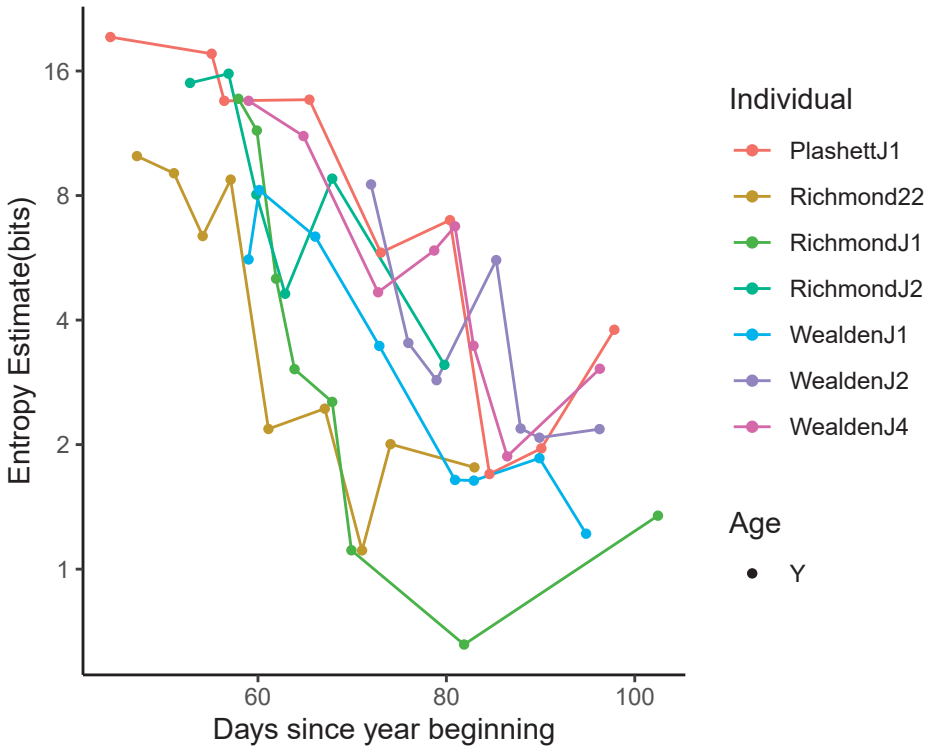


Figure 2.9: Estimates of phrase diversity over the development of 7 yearlings and 2 adults as calculated through a category-less entropy measure. Each point represents an estimated value of syllable entropy for a given individualday, where lower scores indicate the use of fewer unique syllable-types

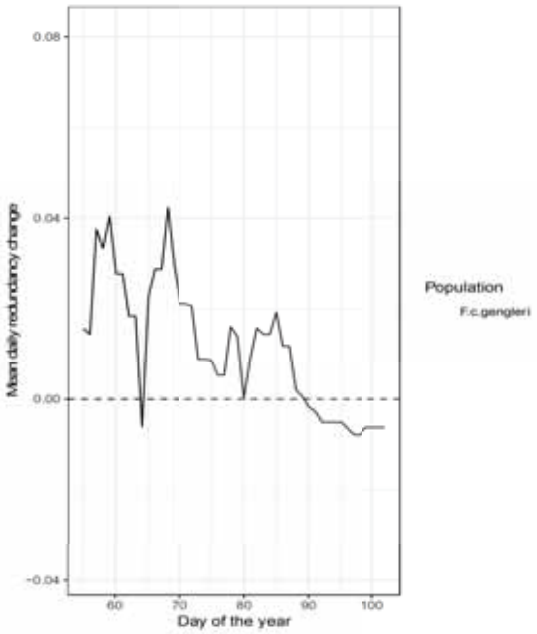


Figure 2.11: Daily rate of change in redundancy across the 7 recorded chaffinches. The mean change in redundancy is represented by the line with the shaded border representing the upper and lower standard deviation of the mean.

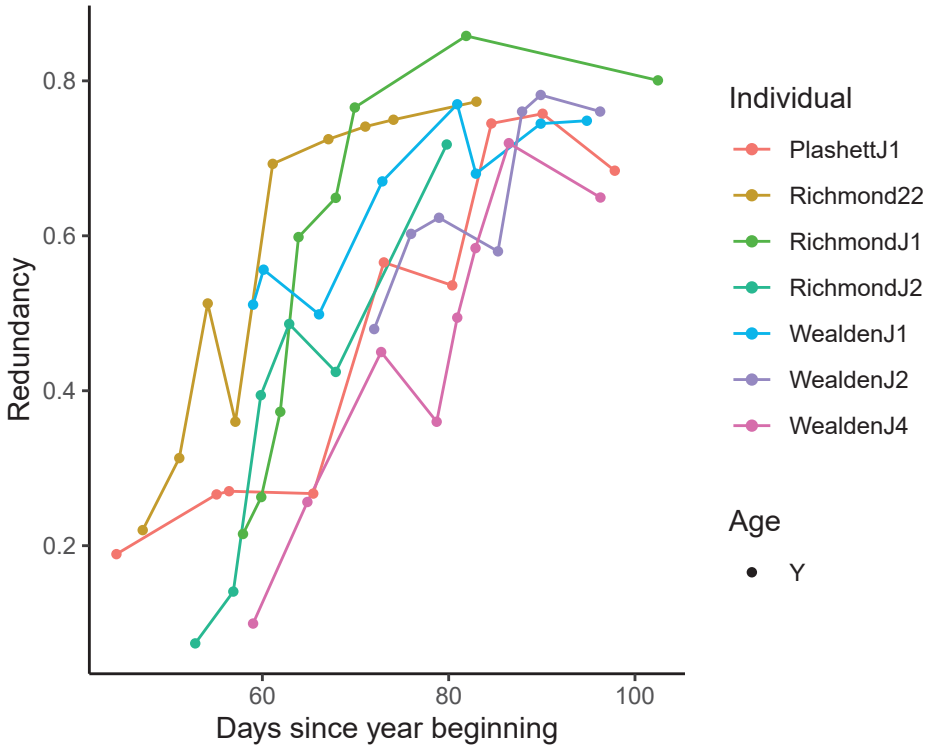


Figure 2.10: Estimates of syllable sequencing consistency over the development of 7 yearlings and 2 adults as calculated through a category-less entropy measure. Each point represents a normalised redundancy score for a given individualday, where a score of 0 would represent syllables constructed in a completely random order, and a score of 1 would indicate no randomness in syllable transactions.

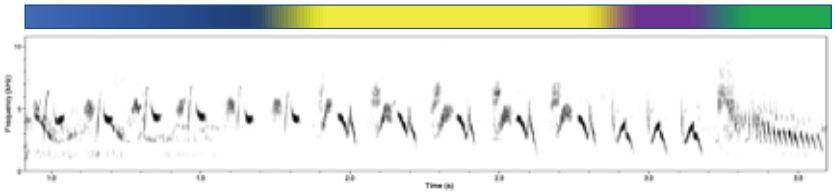
2.3.5 Question 3: The development of phrases relative to sequential position

To examine if phrases were placed in their correct sequential position once they have been phonetically learnt, nested models were produced and examined to see which provided the best explanation in the dissimilarity between a phrase produced by the bird and an exemplar phrase (G^{n+1} and E^{i+1}), given that the phrase G^n was found to be similar to an exemplar phrase E^i in the DTW. The model which best explained the variation was model A4, which included both day of the year, phrase position and an interaction between these. This model had a significantly lower log-likelihood ratio as tested through a chi-squared test than model A3 (Table 2.4). The fixed effect estimate for time was negative (Table 2.5) indicating that for phrases (G^i, G^i ... etc.) which were acoustically like an exemplar phrase (E^i), the dissimilarity between phrases (G^{i+1}) and (E^{i+1}) decreased over time. The models imply that learnt phrases would be more consistently placed into their correct sequence position later in development than earlier. The fixed effect estimate of phrase position was also negative and substantially larger. As the interaction between these two fixed effects was positive, it infers that the later a given phrase is produced within an exemplar song (for example phrase E5 of a song $E^{1\text{-}6}$), the lower the gradient of the dissimilarity change over time between the subsequent phrase of any similar phrase (G^{i+1}) and the phrase following the selected exemplar (in this example E^6). Broadly this indicates that phrases which occur earlier in the song take longer to place into the correct sequence throughout development, whilst later phrases would be more likely to be positioned correctly (see Figure 2.12).

Table 2.4: ANOVA summary comparing LMMs for the relationship between the consistency of phase positioning with developmental time, and the eventual consistent phrase position

Model Description: log dissimilarity (G^{n+1}) <-> (E^{i+1})	df	AIC	Log-likelihood	χ^2	χ^2 df	P(χ^2)
A1: 1 + (1|exemplar)	3	18228	-9110.8			
A2: date + (1|exemplar)	4	16817	-8404.7	1412.24	1	<0.001
A3: date + position + (1|exemplar)	5	16819	-8404.6	0.12	1	0.72
A4: date * position + (1|exemplar)	6	16803	-8395.7	17.93	1	<0.001

(a) Example exemplar 1



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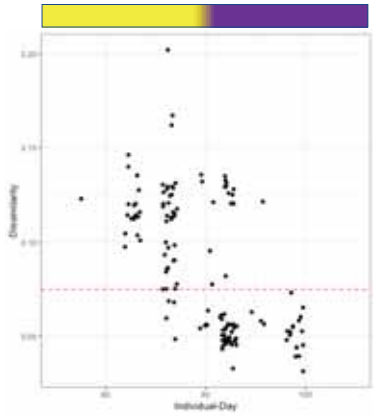

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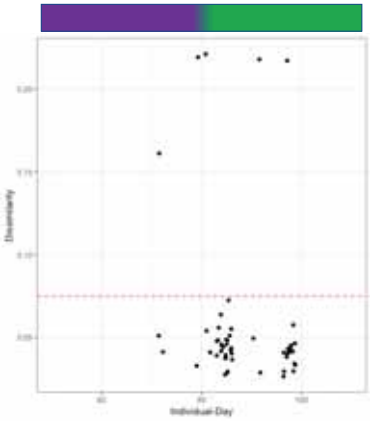
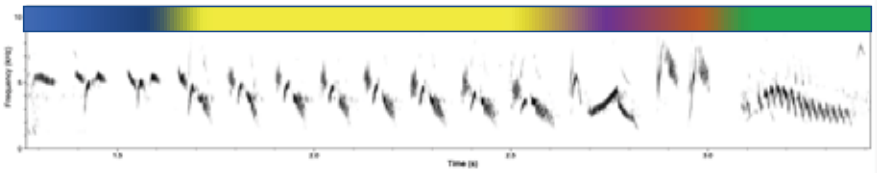


(d) Example exemplar 2



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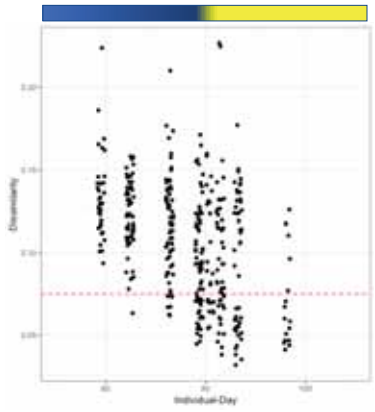

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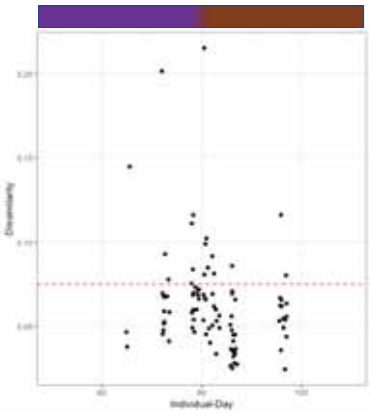


Figure 2.12: Examples (abc, def) of differing patterns of phrase sequencing development in the learning of a single song-type (spectograms a, d) in 2 different chaffinches. Phrase-types are represented by different colours in the bar above each spectogram. Each of the plots b,c,e & f, represents the sequencing of a phrase-pair (phrases with the same colour bar in the above spectogram). Each point in the scatter plot is one phrase produced in development which scored less than 0.075 dissimilarity, with the colour matched by the left-hand colour in the twin-colour bar. The dissimilarity between the next phrase in the developing song and the exemplar (y-axis) is then plotted against the recording date of the developing song (x-axis). The line of 0.075 dissimilarity is plotted in red, and points below this value are occassions where the phrases have been sequenced together in the developing song. The higher the score is above 0.075 dissimilarity, the more likely it is that the phrases have been sequenced incorrectly

Table 2.5: Estimates of fixed effects for model A4 (see Table 2.4)

Fixed effect	estimate	std. error	t-value
(Intercept)	-1.075	0.07	-10.75
date	-0.020	$8.3x10^{-5}$	-26.08
position	-0.074	0.02	-5.15
date: position	0.001	$2.4x10^{-4}$	7.39

2.3.6 Question 4: The development of rhythmic speed and consistency

The rhythmic consistency of yearlings was assessed through measuring changes in the length and clustering tendency of IOI. Increasing day of the year was significantly associated with decreasing IOI times, though the explanatory power of this relationship was extremely small (r^2 <0.015, p= <0.001, n= 54104) (Figure 2.13) On the other hand, the consistency of IOI clustering did also increase during the time period of vocal development, but with a larger effect size (Figure 2.14, Figure 2.15). The inclusion of day of the year into our null model significantly improved its fit (Table 2.6, 2.7), and the positive fixed effect estimate, indicates that IOI timings are more clustered as the date increases.

Table 2.6: ANOVA summary comparing LMMs for change in rhythmic consistency during the development of song in 7 chaffinch yearlings as measured through the Hopkins statistic

Model Description: Hopkins statistic of IOI clustering tendency	df	AIC	Log-likelihood	χ^2	χ^2 df	p(χ^2)
B1: 1 +(1|song)	3	-142.14	74.069			
B2: date +(1|song)	4	-148.82	78.409	8.68	1	<0.005

Table 2.7: Estimates of fixed effects for model B2 (see Table 2.6)

Fixed effect	estimate	std. error	t-value
(Intercept)	0.675	0.04	-14.659
date	0.002	$5.5x10^{-5}$	3.283

2.3.7 Question 5: Song Learning Heterogeneity

To assess whether song-types were learnt heterogeneously, that is where in the development of an individual's repertoire some songs are crystallised earlier than others, I examined the distribution of points in individual dissimilarity scatter plots (Figure 2.16). Each point is a song that was colour-coded by the exemplar song it most closely matched based upon the DTW, plotted over time. Song learning strategy would be indicated based upoon how points were distributed for each exemplar. If one colour was found below the threshold marker for dissimilarity

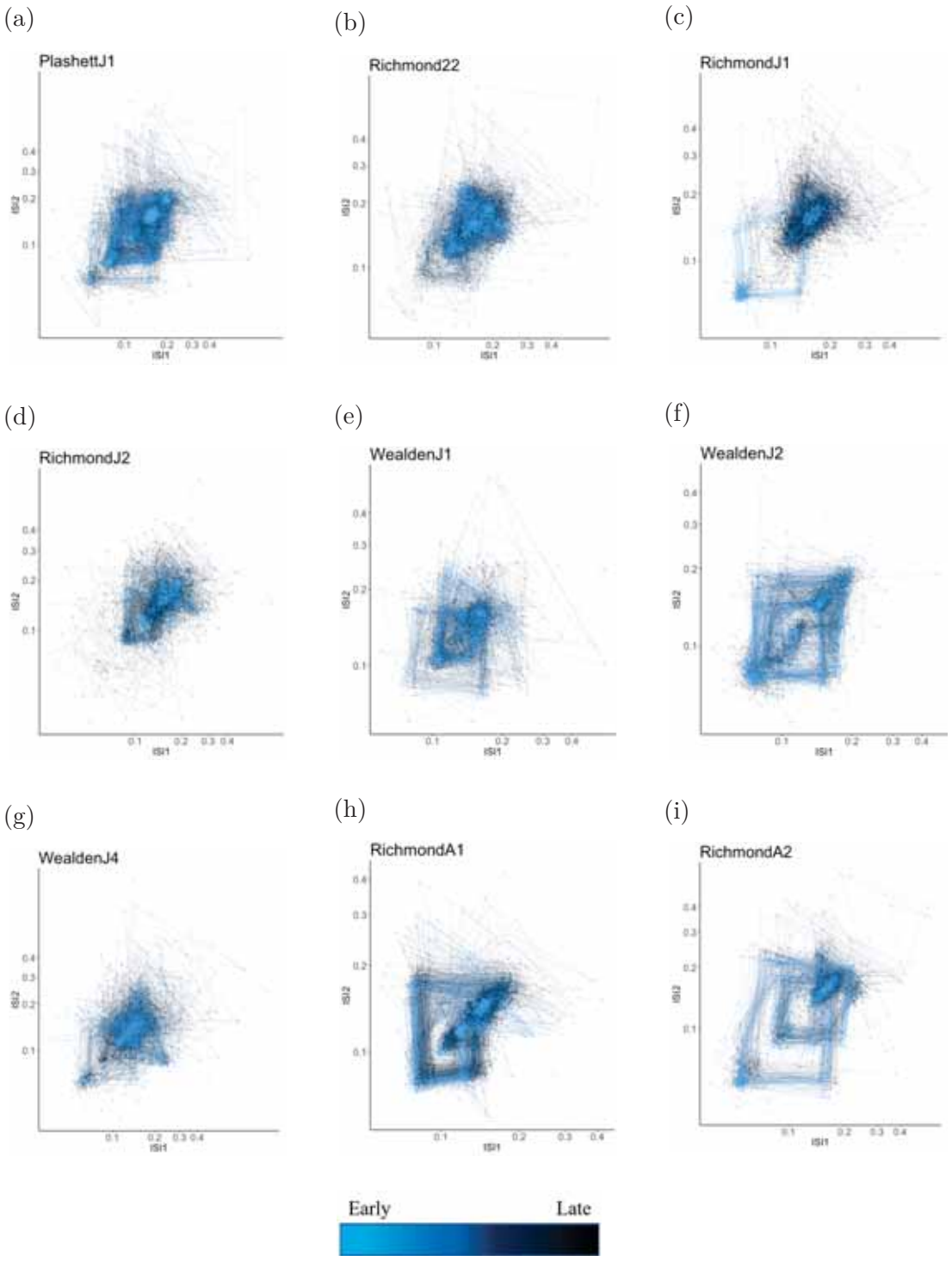


Figure 2.13: Phase space plots calculated on the IOI of syllable transactions for the 7 yearlings (a-g) and 2 adults (h,i) over time. Syllable transitions made by an individual are joined together as a sequence of IOIs (IOI1, IOI2., IOIn). Pairs of adjacent IOIs are then plotted on the x and y axes on a cartesian plane. Lines in between each point represent the change in adjacent points. Points that fall along a 45-degree line (x=y) from origin represent pairs of syllables with equal IOI lengths, with clusters of these points inferring isochronous syllable production. Recording day is indicated with an individual blue colour scale, with darker points earlier recording sessions.

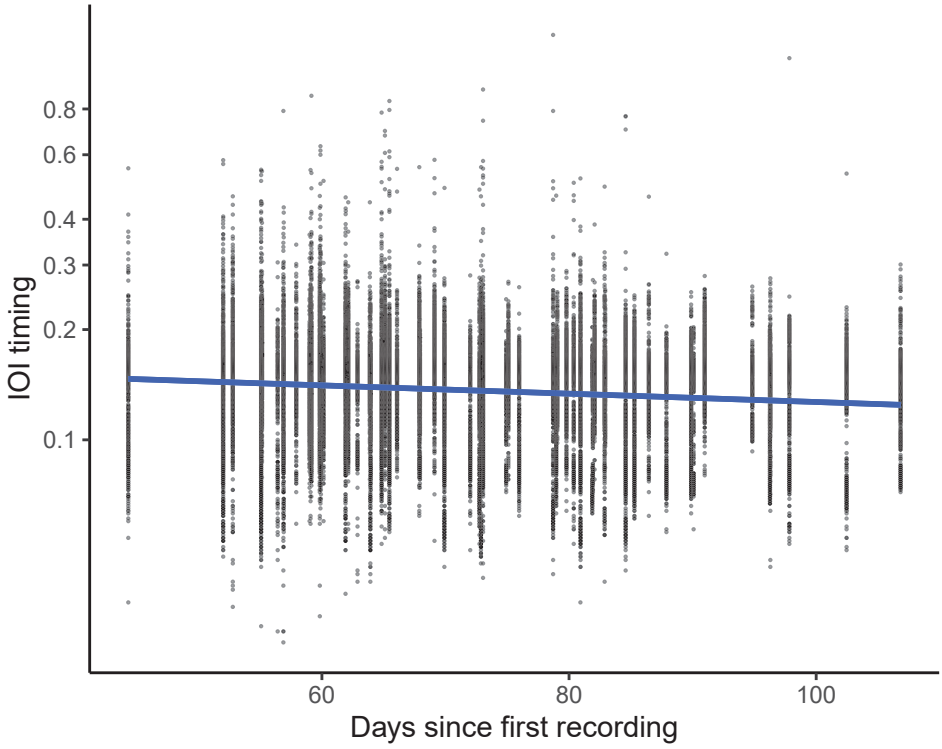


Figure 2.14: Combined IOI timings of song recordings each day for 7 yearlings and 2 adults, with the linear regression of IOI represented by the blue line.

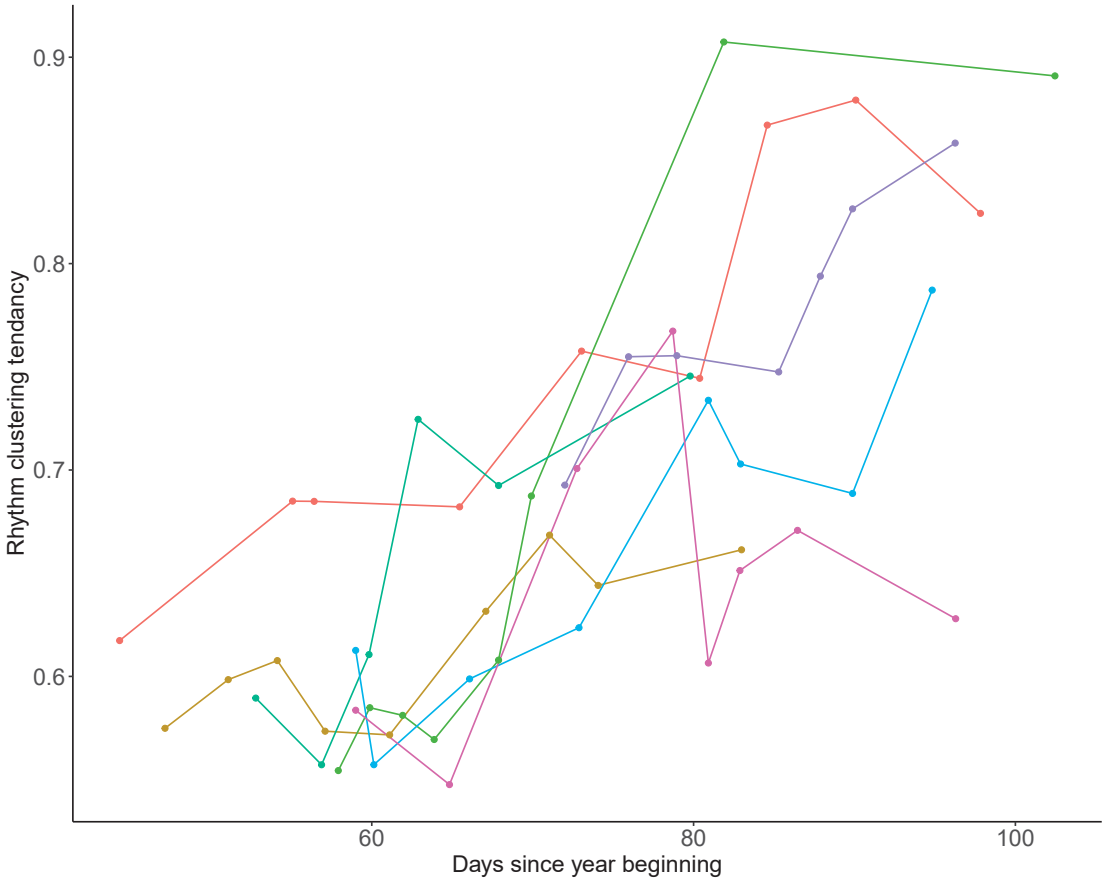


Figure 2.15: Trajectories for rhythmic consistency as measured through the Hopkins statistic on the phase space plots over song development in 7 yearlings.

(0.075) earlier than others, this would be indicative of heterogeneous learning. 6 out of the 7 yearlings showed some evidence of song learning heterogeneity (Figure 2.16). One of the clearest cases occurred in the development of WealdenJ4 (Figure 2.16g), which learned 2 song-types, and produced 28 songs which were measured as being of the same song-type as one of its exemplars, before it produced a single song that matched its other exemplar. The first of these initial 28 matches, came 14 days before the first match to the second exemplar, within which 161 song recordings were made over 4 recording sessions. In this individual, it therefore seems extremely likely that one song-type was acquired before the other. Four further birds produced matches for an exemplar song-type at least one recording session before other exemplars (Figure 2.16b,c,d,e). PlashettJ1 acquired matches for 2 of its exemplars early into its development but acquired its third exemplar substantially later (Figure 2.16a, yellow & black points compared to grey). Only WealdenJ1, first produced close copies of all of its eventual song-type exemplars on the same recording session.

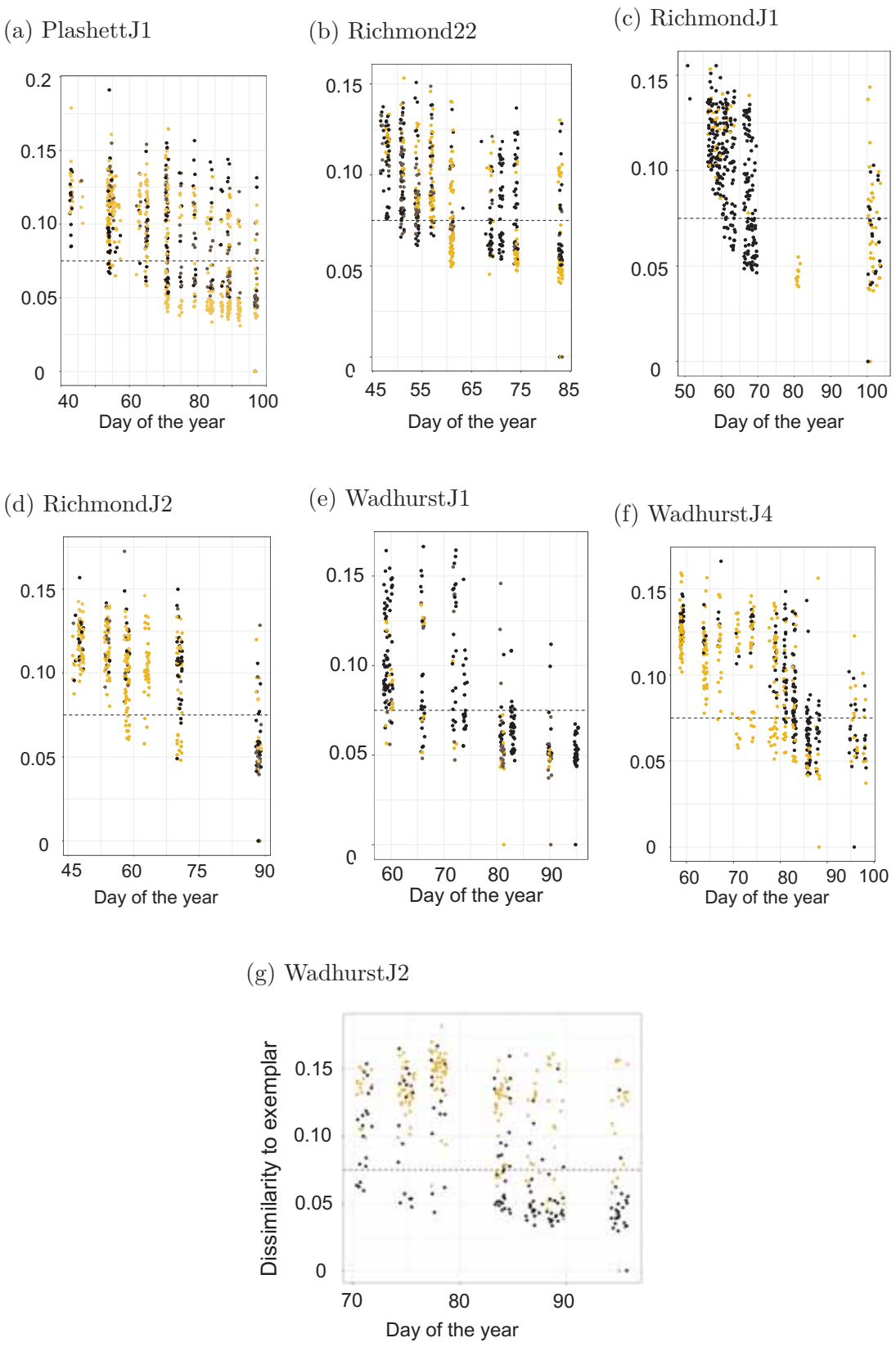


Figure 2.16: Distribution of similarity between songs produced by 7 yearling chaffinches over their vocal development, and the exemplar song they are most similar to. Each exemplar is represented by a colour (colours used: orange, black, grey and brown). Points below 0.075 are classed as belonging to the same-type as an exemplar.

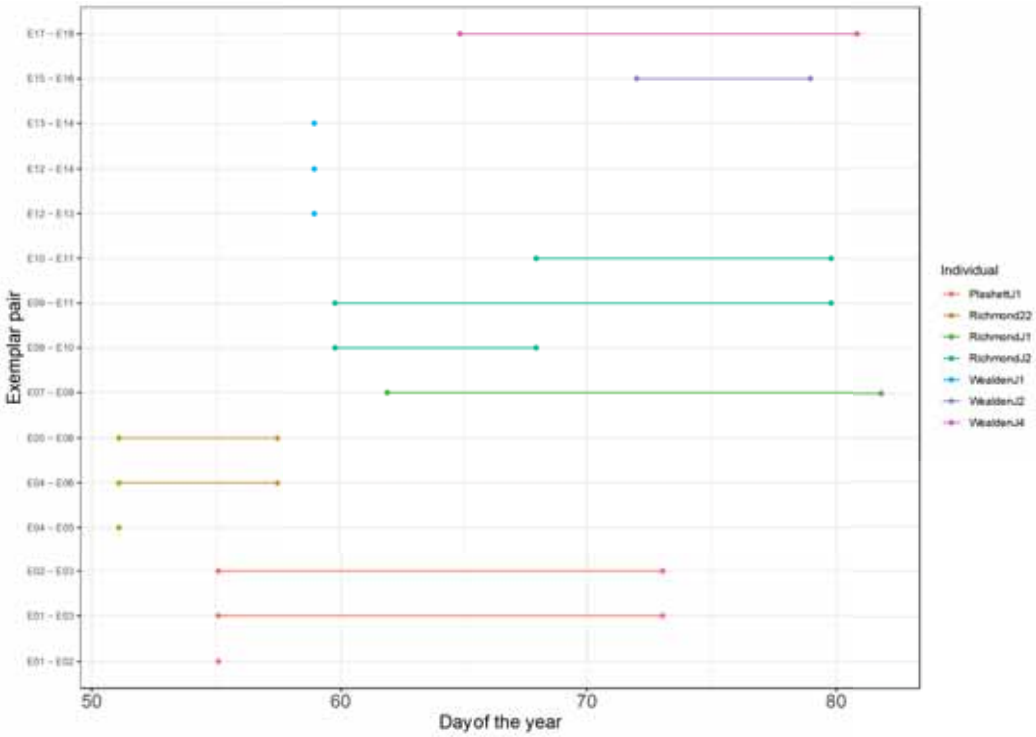


Figure 2.17: Each line indicates the time-gap (in days) the first occassions an individual produced songs which scored less than 0.075 dissimilarity with two different exemplars in the DTW. All possible pairs of exemplars are included, with individuals coloured differently. Points reflect occassions where the individual produced exemplar matches on the same day.

2.3.8 Question 6: Overproduction and selective attrition

Evidence for overproduction was examined in the yearlings through searching for all songs which the yearling did not appear in the yearlings adult repertoire, which scored below a threshold of dissimilarity with songs from another individual. In total, 20 song recordings met this criteria (0.6% of total songs produced). Each of these comparisons was examined manually to confirm that they belonged to the same comparator song-type, and the nature of that song-type compared to other exemplar song-types of that yearling. The findings reported below address these in an individual by individual basis.

2.3.8.1 WealdenJ1

In early recording sessions, Wealden J1 produced 6 songs which were sufficiently similar to a song-type of a nearby adult to be flagged as a potential example of overproduction. From day of the year 59 to 73, the bird included a common song-type for the area in 3 out of the 4 recording sessions (Figure 2.18). The production of the overproduced song was consistent enough that these points tended to cluster (Figure 2.18). Songs from this cluster were greater than the

threshold of dissimilarity from the exemplar songs from that individual. From day 76 onwards, which included 4 sessions and 171 songs, the song-type was not recorded. This song type was also one learnt by other yearlings, WealdenJ2 and WealdenJ3 in a similar timeframe, who held territories less than 2000m away.

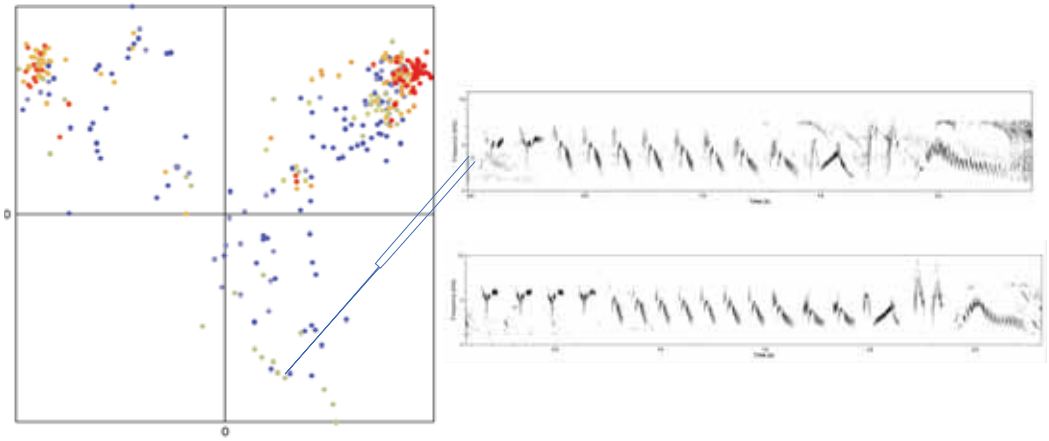


Figure 2.18: NMDS plot for WealdenJ1 accompanied by 2 sonograms, the uppermost being 2.5 seconds in length and the lowermost 3, seconds. Both sonograms are for frequencies 0-10kHz. The first was produced by WealdenJ1 at year-day 65 (as indicated by the colour points associated with that song-type cluster) but subsequently dropped from the repertoire (as indicated by the absence of points coloured yellow-red in that cluster). The bottom sonogram was a song-type produced by a different adult individual in the same year which scored less than 0.075 dissimilarity to the upper spectogram.

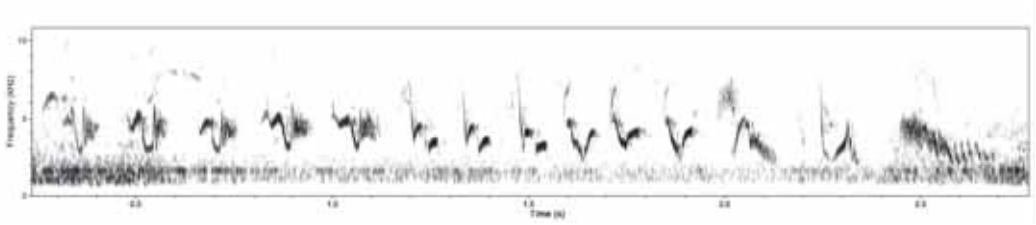
2.3.8.2 RichmondJ1

During stages of RichmondJ1's vocal development, it produced 2 versions of similar song-types (Figure 2.19). Both share a similar structure including an identical flourish, and acoustically similar syllables. In the surrounding adults, several cases of 1 "version" were recorded, whilst none for the the other were found. The version for which no adult exemplars were recorded was the one RichmondJ1 ended up producing during its final 2 recording sessions. 14/26 total song recordings flagged as being overproduced were this song type produced by RichmondJ1.

2.4 Discussion

In this study, I attempted to answer 6 outstanding questions related to the vocal learning of song in songbirds. Firstly, individual chaffinches were able to be recorded throughout vocal development with high certainty of identification and in sufficient detail to allow the remaining 5 questions to be tackled. All yearling

(a)



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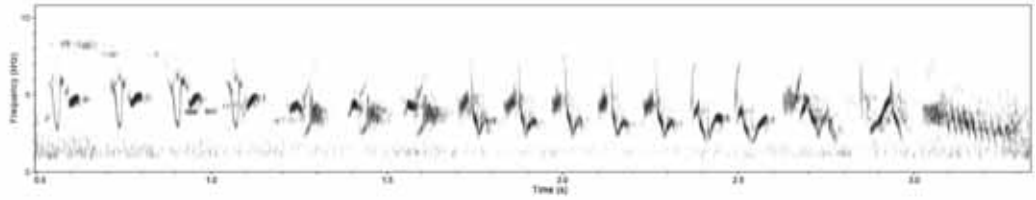

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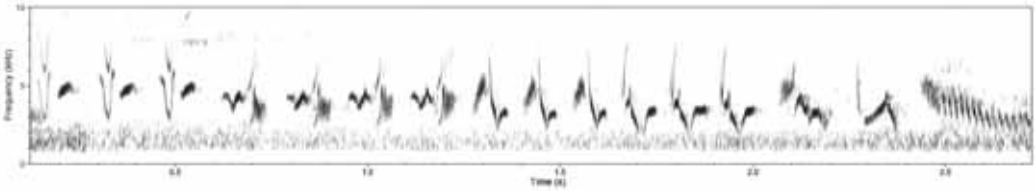


(d) 25/03

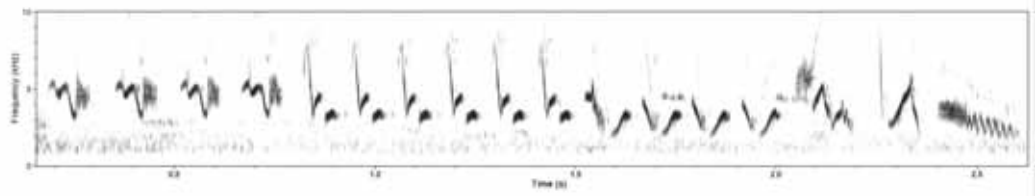


Figure 2.19: Set of sonograms (time 2.5-3s on the x-axis, frequency 0-10kHz on the y-axis), a, b & c produced by RichmondJ1 with d produced by a nearby adult. Pairs a & d and b & c scored below the dissimilarity threshold indicating they were the same song-type. RichmondJ1 produced song-types a and b on day 66 of the calendar year, but only produced song-type d after day 82.

chaffinches exhibited a gradual rise in the predictability of phrase structure and sequencing throughout development, with the peak vocal development occurring between year-days 58 and 72. Exemplar phrase-types varied in the degree to which they were placed in their correct sequential position over development. This was found to be dependent on when the exemplar phase-type occurs in the song; those at the beginning were more variable in their sequential positioning, whereas those at the end of the song are more likely to be sequenced correctly. Rhythmic development was found to occur on two counts. As time progressed, individuals both sped up the rate in which syllables were produced reduced the variance between these time-gaps. Evidence for song learning heterogeneity was also found, with some individuals acquiring some song-types weeks ahead of others. Lastly, overproduction and selective attrition were found to be a rare behaviour in the development of song in chaffinches. In the main, the only song-types developers produced which matched others in neighbouring chaffinches, were songs the eventually retained in their adult repertoire.

The first finding from this study was that wild yearlings could be monitored and recorded over the course of their vocal development. Individual chaffinches were found to share repertoires extremely rarely, as found in other populations (Lachlan, in prep). This means that the singing of identical song repertoires leads to high reliability in identifying individuals. In addition, male chaffinches held singing territories (Marler, 1956a). Anecdotally, I found that territory boundaries were very consistent, across the breeding season.

The comparison of songs between yearlings rendered chaffinches identifiable as individuals, even from their earliest recordings. This is consistent with a number of other studies which utilise acoustic comparison in vocal learners, and point towards a greater potential for this to be used as a non-invasive individual identification marker (Hartwig, 2005; Petrusková, Pišvejcová, Kinštová, Brinke, & Petrusek, 2016). Combined together, the success of these methods indicate there is a high likelihood that vocal development can be measured in the wild in plenty of songbird species, and that these studies can be carried out without invasive capture procedures.

One of the primary objectives of this study was to see if song development in wild chaffinches was similar to previous studies of captive chaffinches (Nottebohm, 1968, 1969a, 1970; Riebel & Slater, 1999a; Thorpe, 1955, 1954, 1958b). Yearlings examined in this study produced songs which matched descriptions of the three main previously described types of developmental song, subsong, plastic song & crystallised song (Konishi, 1965; Nottebohm, 1970; Thorpe, 1958b). However,

based on the results, there was not a clear categorical transition between these types of songs, nor was there a particular time-point where all individuals aligned with a particular developmental song category. Yearlings started defending territories with songs lacking phrase structure or sequential structure, as expected based upon previous field data (Thorpe, 1958b). Then, in general, phrase diversity reduced throughout vocal development, whilst the predictability of phrase sequencing gradually increased. Chaffinches therefore did not develop song in a way which resembled the serial repetition strategy as were found in zebra finches (Liu et al., 2004; Tchernichovski et al., 2001). In relation to phrase development, one further examination which could be explored in this dataset in the future, is whether they used indirect imitation trajectories. Present methods to examine this behaviour have used manual categorisation of syllables into types, which was sought to be avoided in this study due to the high degree of subjectivity which could arise (Tchernichovski et al., 2004). Without this assessment though, it would be difficult to tease apart acoustically similar phrases belonging to different song-types.

It was found that yearlings used mixed strategies to develop high precision of learning of the sequential position of phrases (>93% of song-types learnt were precise copies of surrounding adults, including phrase transitions) , and these strategies could differ even within the song-type itself. These findings fit accordingly with previous evidence for song development in captive chaffinches, where during development, phrases may be sung outside of their correct sequential position during plastic song (Nottebohm, 1969a; Thorpe, 1958b). Along with Lachlan and Slater (2003), this study adds to this notion by suggesting that the likelihood of a phrase being placed out of sequential position is mediated by its intended position.

Whilst the serial repetition strategy has been established to be unlikely to have been used by the chaffinches in this study, the appearance of something resembling the other strategy coined by Liu et al. (2004), motif learning, could be partially considered. Latter phrases were more likely to be positioned correctly in the high majority of cases, and this was particularly true for the penultimate and terminal flourish phrase pair. If this process occurred alongside phrases being learnt concurrently, it could be argued that yearling chaffinches learn their songs "back-to-front", with the ending of the song establishing itself before the beginning. This could be as a result of later phrases being inherently quicker to learn because of their acoustic properties. One further consideration is the relative number of times for which early and late phrases were produced early in development. One recognised feature of early yearling song is that they regularly drop the terminal flourish (Thorpe, 1958b), though there is also evidence that this is a season effect

which impacts all chaffinches (Nürnberger, Siebold, & Bergmann, 1989). It would be of further interest to see if other species which learn their syntactical structure of their song precisely, also learn phrases in a similar manner.

Building on suggestions from Norton and Scharff (2016) for further examination into ontogenic changes in songbird rhythm, we found that two facets of rhythm changed over the course of sensorimotor development in chaffinches. Increase in rhythmic consistency mirrored findings in Bengalese finches (Sasahara et al., 2015) where rhythmic timing clusters would diversify as different pathways of syllable transitions emerged. In addition to this, we found the general speed of rhythmic timings increased, allowing individuals to produce songs at a faster rate.

One question that remains is whether these facets were being developed through a similar sensorimotor feedback to phrase phonetics, syntax etc., or whether this was simply architectural refinement of the motor function required to produce song. Neurological examination of song production revealed motor function of vocal organs occurs in parallel with bursts of action potential in neurons within an individual's HVC (Hahnloser, Kozhevnikov, & Fee, 2002). These combine to produce a clock-like firing pulse (synfire chain) that regulates syllable onset times (Fee, Kozhevnikov, & Hahnloser, 2004; Long & Fee, 2008; Okubo, Mackevicius, Payne, Lynch, & Fee, 2015), though syllable onset may not occur on every pulse (Norton & Scharff, 2016). Though this would be difficult to achieve, assessing the dynamic between tutor, tutor song, alongside a neurological assessment of the HVC over sensorimotor development, would help unpack the level of social cues through which song rhythm is derived.

This study revealed evidence of some heterogeneity in the development of song-types in a chaffinch's repertoire. This might be indicative of particular song-types possessing greater payoffs than others, and therefore are the first which are learned. However, evidence of the function of multiple song-types in the repertoire remains unclear in chaffinches (Brumm, Lachlan, Riebel, & Slater, 2009). There is some support for the notion that some song-type maybe more difficult to produce than others. Within males, some song-types are repeated much more frequently than others (Riebel & Slater, 1999a, 1999b) and different males have been shown to sing bouts of the same song-type for different lengths. Further investigation into the impact, if any, of different song-types on fitness would help ascertain if song learning heterogeneity, resulted in the quicker learning of higher quality song-types.

From a mechanistic perspective, song learning heterogeneity suggests that sta-

tistical learning processes are involved in song development. When the bird is attempting to match syllables, it is producing based upon those stored in its memory, the nature of this random acquisition might lead to one syllable-type being discovered before another. Similar process have been shown in other examples of motor learning (Dhawale, Smith, & Ölveczky, 2017). This in itself might be enough to result in situations where birds fail to produce a syllable-type that matches its inbuilt template until considerably more song renditions have taken place.

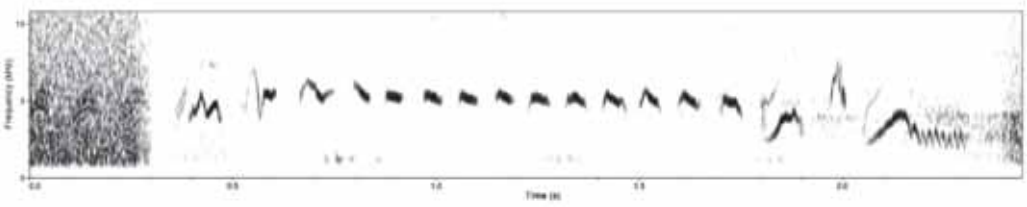
Overproduction of learned songs was not found to occur as frequently, nor for as many song-types in chaffinches as reported in other species (Marler & Peters, 1982; Nelson et al., 1996; Nelson, 1992a, 2000). Findings were comparable to that of (Hultsch, 1991), who placed rates of overproduction at 10% of songs produced by developmental nightingales (*Luscinia megarhynchos*). This difference could reflect an evolutionary change in song development that has occurred between the various taxa. In this case, the most likely destination for this change would occur in the newly distinguished *Passerellidae* which houses the majority of North American sparrows (Klicka et al., 2014), in which overproduction rates are high in some species (Marler & Peters, 1982; Nelson et al., 1996; Nelson, 1992a, 2000), wheras in the remaining members of *Passeroidea*, such as the nightingale (Hultsch, 1991), overproduction is not as prominent. Examination of overproduction rates in further taxa within this parvorder would help ascertain the commonality of this behaviour in song development and allow for more reliable parallels to be drawn between the similarities in attrition behaviour in vocally learning birds and human infants.

My findings could instead reflect a change in the precision in which songs destined for selective attrition are learnt. In the methodology utilised here potentially overproduced songs were compared for dissimilarity with exemplar songs of surrounding adults. However, if attrition were to occur at an early developmental stage where any song produced would not resemble the adult songs closely, then the methods I used would fail to detect selective attrition. In particular, it would be interesting to consider overproduction at the level of individual syllables.

The earliest suggestion for overproduction to occur in chaffinches was the removal of heterospecific song (Marler, 1956c). One factor in my analysis is that the dissimilarity matches were made with surrounding adult chaffinches, and not other heterospecific songs. In general, it was the case that subsong and plastic song resembled chaffinch songs more than any heterospecific song. However, an individual case, WealdenJ4, was an exception. Over the first 4 recording sessions,

the bird would incorporate high pitch, repeated syllable types in large portions of songs, in a rhythm that resembled those of a blue tit *Cyanistes caeruleus* (Figure 2.20a). After year-day 71, the bird was not heard to produce this song type again, and this date corresponded with the bird increasing its song redundancy also. This would imply the bird had used selective attrition to remove heterospecific sounds from its repertoire. However, if this were the primary function of overproduction, then we would expect no heterospecific song to be produced by adults. Of the 98 adults recorded in this study, 2 possessed songs closely resembling those from other species. An individual in Plashett Wood also produced a blue tit-like song (Figure 2.20b). This individual lived 21.67km away from WadhurstJ4 and therefore is therefore unlikely to have been a tutor. A second adult individual in Richmond possessed a song-type more acoustically reminiscent of greenfinch *Chloris chloris* than of a chaffinch, a species had been previously recorded as having its song incorporated into adult chaffinch song (Conrads, 1977). With this in mind, if the function of selective attrition was to remove heterospecific material, then it is not successful in all individuals.

(a)



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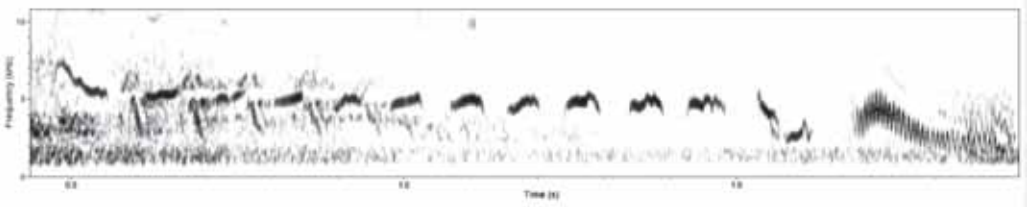


Figure 2.20: Spectrograms of possible heterospecific song producing by chaffinches. A) was produced regularly by a yearling, whilst b) was recorded in an adult from another population.

In summary, a range of fieldwork and analytical techniques have been developed that allow for the development of song to be measured and compared in wild individuals. Such methods could now be readily utilised to answer further outstanding questions regarding vocal learning. One area for which developmental comparison is currently under-utilised is within the evolution of song (Beecher, 2008). Replication of these methods could allow for examination of how changes in life history, ecology and other environmental factors impact song developmental

strategy, end of development song organisation and the precision of song learning.

2.5 Conclusion

Observational and experimental assessment of data from laboratory-reared songbirds produced convincing arguments for the processes underlying the development of song. Direct evidence of developmental trajectories in wild birds had been absent prior to this study. The findings presented here indicate a gradual shift from an initial production of unstructured subsong towards more phonologically and temporally structured songs, which eventually arrives at crystallised song, equivalent to that of older males. Birds were found to sequence phrases using multiple strategies, with phrase-types eventually placed at the beginning of crystallised songs, much more variable in positioning than phrase-types eventually placed at the end of crystallised songs. Rhythmic timing was found to get quicker and more consistent over the course of development, and there was also good evidence for heterogeneity in song-type development. Finally, overproduction and selective attrition were found to be rarely utilised in chaffinch song development. These findings indicate that methods utilised were successful in exploring a range of outstanding questions on development, and potential future use on other species for comparative analyses which explore the relationship between song development and the evolution of song.

Chapter 3

On the evolution of vocal development in island chaffinch populations

Abstract

Young songbirds acquire songs through vocal imitation and each songbird learns to produce songs under rules unique to that species. Factors such as evolutionary history, life history and species ecology are thought to play a role in how these songs evolve, but we are yet to understand the dynamics behind this. Here, I use a novel approach for comparing song learning differences between populations, through analysing developmental trajectories of wild songbirds. Members of the chaffinch genus *Fringilla* were examined; *Fringilla coelebs gengleri* from Great Britain (see Chapter 2), and two Atlantic Island populations, *F.c.canariensis* and *F.teydea*. Prior research has indicated that song learning in *F.c.canariensis* is the least precise overall, and that whilst *F.teydea* learns songs precisely, it has a lower repertoire size than *F.c.gengleri*. 7 first-year males from each population were recorded systematically throughout their sensorimotor development. Song syllables were compared computationally using a dynamic time-warping algorithm, and the stereotypy of phrase sequencing compared through a threshold-based match-less entropy measure. All *F.coelebs* yearlings were initially recorded with songs lacking stereotyped sequence structure. However, both Tenerife chaffinch species developed songs more slowly and over a significantly longer period than the British birds. The most rapid phase of song development in *F.c.canariensis* also occurred significantly later than in *F.c.gengleri*. Similarly to the British chaffinch, *F.c.canariensis* did still show development of rhythmic consistency throughout the

sensorimotor phase, which was not found to occur in *F.teydea*. This first attempt to compare the development of song in wild populations therefore revealed that slower development, may be a potential mechanism through which song learning evolves.

3.1 Introduction

3.1.1 The maintenance of song diversity

The oscine songbirds are one of the few groups of animals to have evolved vocal learning, with each species developing songs with characteristics unique to that species (Beecher & Brenowitz, 2005; Jarvis, 2004). Casual observers and ornithologists alike have been fascinated by the similarity of song learning within species, and yet how differently closely related species can sing (Brenowitz, 1997; Catchpole & McGregor, 1985; Irwin, 2000; Marler, 1970; Podos, 1997; Podos & Warren, 2007; Read & Weary, 1992). Despite song learning possibly contributing to the acceleration of evolution of the songbird radiation (Kroodsma & Miller, 1996; Lachlan & Servedio, 2004), the question of how song learning evolves remains unanswered (Catchpole & Slater, 2008; Slabbekoorn & Smith, 2002a). Previous attempts to examine this have largely focussed on *what* song components birds learn. Far fewer studies compare *how* birds learn (Beecher, 2008). Due to the difficulty in examining song development (Liu & Kroodsma, 2006; Mennill et al., 2018), comparative assessments of this process have previously been restricted to the laboratory (Nelson, Marler, & Palleroni, 1995), or only examining developmental end-points (Marler & Peters, 1977) or grouped songs recorded over development together (Roper et al., 2018). These all carry limitations which could result in key developmental processes being overlooked; in the case of captive individuals due to their limited social environment, and grouping songs over development the detail for which different stages of song development have been captured in a single individual. Here I address this, by performing the first comparison of vocal development in wild individuals, through examining three evolutionarily distinct population which appear to have diverged in how they develop songs.

Songbirds studied to date have been found to acquire their songs through a two-stage process early in life (Catchpole & Slater, 2003). In an initial sensory stage, young birds listen to sounds in their environment, select songs that match an inbuilt template, and store them in long-term memory (Marler, 1970; Nottebohm, 1968). Then in the sensorimotor stage, juveniles guide their own vocalisations

towards these memorised templates, through a period of self-guided auditory feedback (Konishi, 2004; Liu et al., 2004; Marler & Peters, 1981; Nottebohm, 1968, 1970; P. H. Price, 1979; Tchernichovski et al., 2001; Thorpe, 1954). During this period of plastic song, some species have been found to produce far more songs than typical adult repertoire (overproduction), and go through a process of selective attrition, gradually reducing the size of their repertoire to one more typical of adults (Marler & Peters, 1981, 1982; Nelson, 1992a, 2000). In many other species, a distinct time point then signals the end of the sensorimotor phase, after which an individuals' songs are unlikely to change (Nottebohm, 1969a; Thorpe, 1958b), though there is some indication that further auditory feedback is required to maintain song structure (Lombardino & Nottebohm, 2000; Okanoya & Yamaguchi, 1997). These songs are deemed to have crystallised. In this study, I will focus upon comparing the difference in the sensorimotor phase; and in particular how songs produced change over time and timing of crystallisation.

The degree to which young birds select song features from their own species has been explored through exposing individuals to different types of song and examining what they learn. Typically individuals will only learn songs produced by their own species (Marler, 1970). However even those which only rarely demonstrate heterospecific mimicry such as the chaffinch *Fringilla coelebs*, can be trained to learn songs from other species through selective exposure (Baptista & Morton, 1988; Baptista & Petrinovich, 1986; Slater, 1983; Thorpe & Pilcher, 1958). Marler and Peters (1977) found that male swamp sparrows *Melospiza geogiana* learnt songs containing conspecific syllables, even when produced in the more complex organisational pattern of the heterospecific song sparrow *Melospiza melodia*. *M.geogiana*, which develop songs comprising of a solitary repeated syllable, failed to utilise any *M.melodia* syllables into their song. On the other hand, *M.melodia* did learn to place *M.geogiana* syllables into their song, and were more likely to do so if they were presented in a syntactical structure more typical of *M.melodia* (Marler & Peters, 1988). This provided the first evidence of an evolutionary divergence in song development, and how different song components (phonetics, syntactical structure) can change in their importance even in closely related species.

Alongside these end-of development assessments, more detailed examinations of the process of song development has also revealing changes in patterns of learning behaviour, even within species. Nelson et al. (1995) performed a broader assessment of song development in captive migratory and sedentary subspecies of white-crowned sparrows *Zontrichia leucophrys*. They found that the migratory *Z.l.oriantha* spent significantly longer producing plastic song than the sedentary

Z.l.nuttalli, whilst crystalisation occurred at a wider range of ages than found in *Z.l.oriantha*. Through the use of spectrogram cross-correlation (Clark et al., 1987), they also found that *Z.l.nuttalli* males imitated tutor syllables more accurately than *Z.l.oriantha*. Nelson (1999) added to this through examining the development of songs in another migratory subspecies, *Z.l.gambelii*. He found that whilst this subspecies also overproduced songs like other *Z.leucophys*, they appeared to pick their songs at random, rather than matching to any particular neighbour as found in *Z.l.nuttalli* and *Z.l.oriantha*. From these series of studies, the authors made inferences how subspecies ecology was impacting the timing of learning, and how this affected the speed and precision within which song components are learned. However, in their experiments developing individuals were kept in atypical social environments, and analysis was largely limited either to time spent during certain developmental phases, or qualitative differences between the songs yearling birds learn and surrounding adults. A more detailed analysis of development, incorporating acoustic changes, as well as other key components of song would provide a more thorough picture of links between species ecology and the evolution of song.

The precision through which young birds mimic adults also varies greatly between species. The model species for studying song learning, the Zebra finch *Taeniopygia guttata*, rarely learn all of the song components present in the tutor song (Holveck et al., 2008; Jones & Slater, 1996; Mann & Slater, 1995). Whereas other species learn so precisely, that their songs can persist in the same form for hundreds of generations (Lachlan et al., 2018). Sequential structure is another component which can change in how precisely it is learnt. Some species, such as the chaffinch, have as little error rates as 1% in learning both the components of the song, as well the order in which those units were sung (Lachlan & Slater, 2003). With every additional unit in a song's sequence, the possible combinations of unit transitions a bird must remember multiplies exponentially, inferring a higher energetic cost during development (Lipkind et al., 2017). As a result, examining related populations which differ in how predictably they transition between song units would provide the ideal opportunity to compare how these differences develop.

3.1.2 The evolutionary history of the chaffinch

One such example occurs in the chaffinch. The species is widespread across continental Europe, where it learns to produce songs usually formed of between 5-7 phrases (Figure 3.1). Each phrase contains one syllable-type, with the beginning phrases often containing repeated renditions of the syllable-type, whilst the later

phrases include less repetition, ending with a buzzy flourish phrase (Figure 3.1). Across its continental range, the general structure of chaffinch song is remarkably similar (Marler, 1952; Slater et al., 1984; Slater & Ince, 1979). Alongside these, at least five genetically distinct subspecies of chaffinch are distributed across the Atlantic Islands (Delgado et al., 2016), which have been isolated from the mainland population for at least 400,000 years (Marshall & Baker, 1999), as well as two sister species, *Fringilla teydea* and *Fringilla polatzeki*, which were the product of an earlier colonisation event (Lifjeld et al., 2016; Sangster et al., 2016). *F.coelebs* is thought likely to have colonised the islands in a sequential manner from neighbouring Iberia; arriving first to the Azores before reaching Madeira and latterly the Canary Islands.

It has long been noted that these island *F.coelebs* sing differently to continental birds (Searcy & Yasukawa, 2014; Thorpe, 1958b). Lynch and Baker (1993) produced one of the first analytical comparisons of the differences between continental and island chaffinches, where they compared the diversity of phrase sequences of varying lengths (Lynch & Baker, 1993, 1994). The diversity of phrases in the islands was found to be no higher than would be expected in a continental population. However, the diversity of phrase sequences was significantly higher in the islands than in the rest of Europe. One inference that might be drawn from these results is that learning precision was lower in the island populations, with chaffinches instead "mixing and matching" phrases from various tutors together to generate novel songs (Lynch & Baker, 1994; Riebel et al., 2015). Further evidence of song learning changes came in Lachlan et al. (2013), who found evidence of increasingly relaxed syntactical structure in a pattern which matched the expected colonisation route. Thus, island chaffinches both learn their songs less precisely than mainland birds and are more relaxed in the structure of the songs that they will learn. This makes the chaffinch genus *Fringilla* an ideal target for examining the evolution of song.

Having examined the development in a chaffinch subspecies representative of mainland Europe in Chapter 2 (*F.c.gengleri*), in this chapter I compare their development with two further populations of chaffinch in the Atlantic Islands. The first population assessed, *F.c.canariensis*, a subspecies of chaffinch found in the central Canary Islands. Tenerife common chaffinches have some of the lowest precision rates of learning of any chaffinch population (Lynch and Baker (1993, 1994); Lachlan in prep), as well as being the most variable song syntactical structure Lachlan et al. (2013).

The second population to be analysed is the Tenerife blue chaffinch *F.teydea*. Un-

like its critically endangered cousin on Gran Canaria, *F.teydea* is fairly widespread, rendering Tenerife the only location in the world where 2 chaffinch species are common (Lifjeld et al., 2016; Sangster et al., 2016). Genetically, *F.teydea* is most closely related to the spodiogenys haplotype of common chaffinch from Northern Africa, with mtDNA data placing a likely colonisation date at roughly 2mya (Rando et al., 2010). Unlike *F.c.canariensis* on Tenerife, it is not believed to have undergone successive colonisation events to have reached the island (Rando et al., 2010).

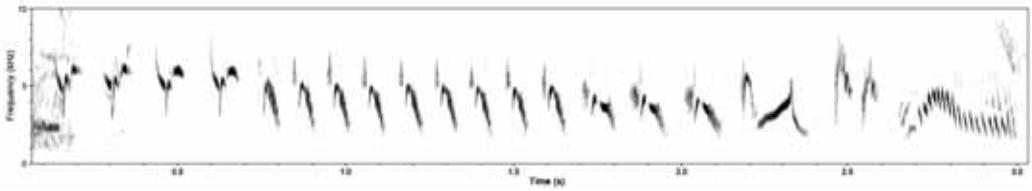
F.teydea breeds exclusively in Canarian Pine forests, and though these are typically higher in altitude than those occupied by *F.c.canariensis*, there is an intermediatory zone where both species hold territories (Slater & Catchpole, 1990). Ecologically, the breeding conditions that both species face are therefore fairly similar and are characterised by low seasonality, low predation and low heterospecific competition (Carrascal, Telleria, & Valido, 1992; Fernández-Palacios et al., 2011). These conditions are much more tropical than others occupied by chaffinches, with the Canary Islands also comfortably the lowest latitude in which chaffinches breed.

In terms of songs, unlike the two subspecies of *F. coelebs*, the modal repertoire size of *F.teydea* is just 1 (Lifjeld et al., 2016). Their songs are often regarded as being 'simpler' than *F.coelebs*, nearly always beginning with a series of repeated notes and ending on one-three buzzy notes (Figure 3.1c). Whilst less well studied than *F.coelebs*, population level analyses has revealed precise learning of whole song-types (Lachlan, in prep). Given that the low numbers of phrases used by *F.teydea*, and how all males recorded possess similar song structure, it seems likely that sequential structure is high, though no prior analysis of this has yet been conducted. Overall, as a triad of study species, these three offer a broad range of colonisation histories, ecological specialisation and song learning strategies (as summarised further in Table 3.1). Through comparing the development of song features between them, I aim to infer which external conditions have impacted the production of song in these species. A particular focus will be placed upon the development of song sequential structure, for which three hypotheses will be used to test already established differences between two of the three study populations.

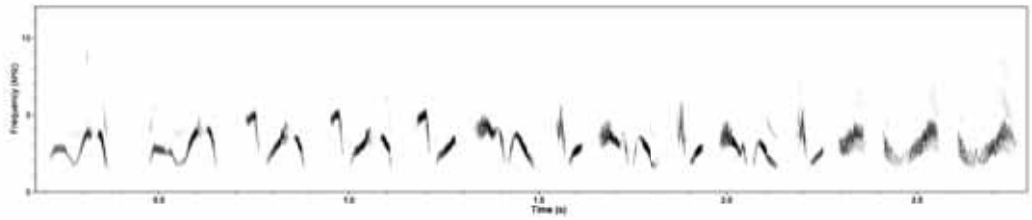
3.1.3 Hypotheses

I will compare the trajectories of development in the three *Fringilla* populations for three features of song, phrase entropy, sequential structure & rhythm, but will pay a primary focus on sequential structure. Sequential structure will be

(a) *F.c.gengleri*



(b) *F.c.canariensis*



(c) *F.teydea*

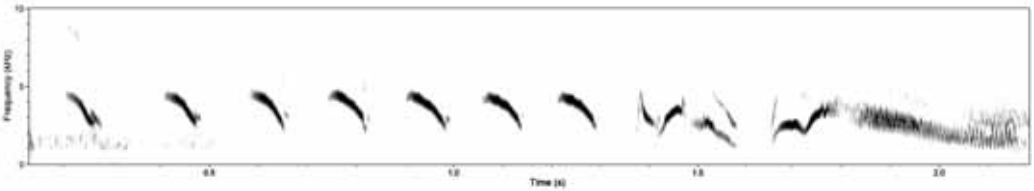


Figure 3.1: Three representative songs produced by adult males in the selected study populations.

Table 3.1: Brief summary of study population similarities and differences

Scientific Name	*F.c.gengleri*	*F.c.canariensis*	*F.teydea*
Typical song repertoire size	2-4	Anywhere from 1-6+	1, occasionally 2
Precision learning of song-types	Yes	No	Yes
Sequential structure learning	High	Low	Likely High
Neighbour song sharing	Low	High where present	High
Location	South-east England	Tenerife	Tenerife
Colonisation Date	$<$ 30,000 ya	c. 400,000 ya	c. 2,000,000 ya
Colonisation Origin	Pleistocene refugia	Northern Atlantic Islands	Northern Africa
Habitat	Temperate mixed	Laurel forest	Pine forest
Seasonality	High	Low	Low
Predation Risk	High	Low	Low

analysed through examining change in phrase redundancy over time (see Chapter 2 for details). Four possible hypotheses (Figure 3.2c) of changes in developmental trajectories will be used to compare differences between the learning of song in the Canarian populations, relative to the trajectories of sequential structure reported for *F.c.gengleri* in Chapter 2.

The **null hypothesis** is that there will be no difference in developmental trajectories, with individuals acquiring adult-typical levels of sequential structure over a similar time period, at a similar rate (Figure 3.2c, blue). A second hypothesis is that *F.c.canriensis* yearlings could "crystallise" earlier in development than a time point in which they would be able to reproduce song types in full (Figure 3.2c, grey). It has already been demonstrated that an early administration of testosterone can result in premature crystallisation of simpler songs (Templeton et al., 2012). This will be referred to as the **early crystallisation hypothesis**. Similarly, low redundancy singers may be a product of delayed early development, or lower initial redundancy scores (Figure 3.2c, yellow). For a potential example, perhaps due to greater vocal architecture, Tenerife birds are able to produce a greater array of sounds than British birds but are only able to reduce errors at the same rate as British birds. Despite learning at the same rate, crystallisation occurs too early for the majority of Tenerife birds to reach high redundancy levels. This will be referred to as the **sluggish starters' hypothesis**.

A separate prediction, referred to as the **slow learning hypothesis**, the rate of increase towards adult level sequence stereotypy is slower than would be expected of a British chaffinch (Figure 3.2c, blue). For this to be the case, the gradient of developmental trajectories would have to be lower in Tenerife birds compared to British. It could be speculated that this could occur either through an elongation of an individual's sensorimotor development, or as an absence of periods of rapid gains in song stereotypy, as found in British birds (as found in Chapter 2).

Alongside these hypotheses, comparisons of developmental trajectories will also be examined in regard to the consistency in phrase diversity and syllable rhythm. Rates of overproduction will also be tested in *F.teydea*, as unlike *F.c.canariensis* this species learns song-types in full. High neighbour song-sharing rates and low repertoire size are common features of the North American sparrows which do possess high rates of overproduction. In the previous chapter, it was found that this behaviour was rare in *F.c.gengleri*.

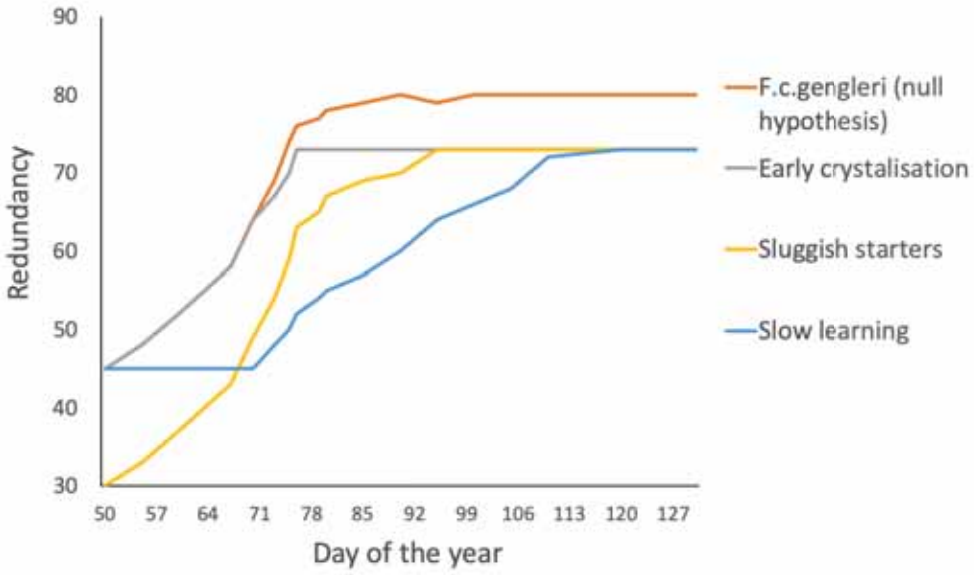


Figure 3.2: Four developmental trajectories reflecting the sequential structure of chaffinch songs throughout their development. The trajectory in orange is representative of changes in sequential structure found in Chapter 2. The three remaining trajectories reflect predictions for how Canarian chaffinches might develop differently, as outlined under the early crystalisation, sluggish starters and slow learning hypotheses. In the early crystalisation hypothesis (grey), development begins similarly to that of *F.c.gengleri*, but the bird crystalises prematurely, preventing further increases in sequential structure. In sluggish starters (yellow), vocal learning begins with less sequential structure than found in *F.c.gengleri*. For slow learning (blue), the rate of sequential structure change is lower than that of *F.c.gengleri*. A lower level of redundancy at the end of development is also predicted for *F.c.canariensis*, due to its higher repetoire size.

3.2 Methods

3.2.1 Field recordings

Chaffinches were monitored each spring between February 2015 and April 2018. Study sites were selected such that they offered suitable breeding habitat for the respective population assessed. Yearling *F.c.canariensis* were recorded on Tenerife in Spring 2016, specifically in the Parque rural de Anaga (28.520, -16.280) and the Eastern Corona Forestal National Park in Tenerife (28.446, -16.385). Adult birds were recorded in 2018, in the area of La Montaneta (28.338, -16.761). *F.c.gengleri* were recorded across South-East England in United Kingdom, around Richmond (51.477, -0.286) in Greater London during 2015 and Plashett Wood (50.932, 0.065) and Wadhurst Park (51.065, 0.0271) in East Sussex in 2017. One *F.c.gengleri* individual was also recorded during the Spring of 2018 in the Richmond area. All yearling *F.teydea* were recorded in the Western Corona Forestal National Park (28.173, -16.629) in Tenerife, Canary Islands in 2018.

The first task for data collection was to detect yearlings, which needed to be done as early as possible from when they would begin defending territories. Initially, field transect sampling took place to monitor natural singing activity of chaffinches with peak activity occurring between 20 minutes before sunrise and 13:00 hours. After every 100m for which a chaffinch was not visibly or audibly detected, playback of either chaffinch contact calls or heterospecific songs, were broadcast from wireless speakers (UE Boom 2, Logitech). This was used to lure birds towards an observer for visual inspection. In the islands chaffinches, *F.c.canariesnsis* and *F.teydea* engage partial moults during their first winter (Collar, Newton, Clement, & Arkhipov, 2010; García-Del-Rey & Gosler, 2005) and are therefore visibly distinguishable from older adults. Primarily, these distinctions are visible in the mantle, with yearlings lacking the uniform indigo to dark grey feather patterns in both species. *F.teydea* yearlings are predominantly brown with bluer face colouration and *F.c.canariensis* yearlings possessing a brown - green mantle.

As with all yearlings, the other distinguishable feature was their regular production of subsong. In *F.coelebs* subsong differs from adult song, as no particular syllable is ever repeated. These differences in consistency can be recognised by a trained observer whilst in the field. In *F.teydea* similar was expected, but unlike *F.coelebs* no prior analysis or recording evidence of subsong has been described, or was found available in online song repositories (such as www.xeno-canto.org). As the majority of *F.teydea* males produce 1 song type in adulthood, any bird that was heard producing multiple song types was then assessed visually.

A number of measures were put into place to ensure that the same individual was recorded during each recording session. In spring chaffinches are highly territorial, and only sing within specific areas of c. 100m^2, though this can increase substantially in low quality habitat (Marler, 1956b). Within these territories, individuals will select perching points from which to sing, though many suitable sites are available. Therefore, the repeated occupation of the same perches across multiple visits would also indicate the same individual was present.

The locations of all yearlings detected were recorded using a handheld GPS device (Iphone 6s, Apple). If a yearling was detected within 10m of previously observed perching points in a subsequent visit, the territory was considered to be occupied by a yearling. Weather permitting, the territory would be visited every subsequent 2-3 days, with recordings made of the territorial male until the bird produced consistent song output on multiple visits. Recordings were made using a TASCAM -DR100 MKII and Telinga Pro-8 Twin Science Microphone positioned within a Telinga parabola of 570mm diameter. Recordings were digitized at a sample rate of 44.1 kHZ onto a SanDisk USB soundcard. Distance between the microphone and individual recorded varied between 2 - 20m. For each territory visit, we aimed to record 50 complete song renditions, as this would be sufficient to make sure all songs in an adult repertoire were recorded.

In addition to yearling males, we recorded surrounding adult males in solitary 50-song recording sessions. These served as a baseline for songs already present within the population that the yearlings would have memorised in their sensory phase and allow us to compare how precisely syllable transitions in these songs were copied by the yearlings. From these 2 adults per population were selected to further record throughout the period in which yearlings were developing, to serve as baseline comparators for how adults produce songs over a comparable time of the year.

3.2.2 Song processing

All recordings were processed through the software package Luscinia [Version 2.17.11.22.01 rflachlan.github.io/Luscinia]. Through the "Add recording" function, songs were isolated from background noise, and segmented into individual files. For each song, the "Make spectrogram" function was utilised to present songs as sonograms with standardised settings (for parameters see Table 3.2). Song elements, defined as singular units of continuous signal, which were produced by the targeted individual, were traced away from background noise through visual inspection of the sonogram by a trained observer (JC). Song units were

manually placed into syllables; in both chaffinch species, we defined a syllable as a singular or collective unit of sound interspersed by silent intervals of 10ms or greater. Syllables which appeared visually similar to an adjacent syllable were then manually grouped into repeated-syllable phrases, with individually distinctive syllables considered a unique-syllable phrase. Song recordings which had excessive background noise, low recording quality or contained multiple individuals were not measured.

For each song element traced, Luscinia measures multiple acoustic features for every time-step in the spectrogram to produce contours for how each feature varies during the timespan of an element. Here, the measures included time, fundamental frequency (FF herafter), FF change and vibrato amplitude. FF change was calculated by conducting an arctan transformation on the slope of the element (Lachlan et al., 2013), with a parameter weighting of 0.02 applied. Vibrato amplitude was calculated as the maximum and minimum peak in the frequency domain.

Once all songs had been processed, datasets consisting of any desired combination of songs could be compared. These comparisons were made using the implementation of a dynamic time-warping algorithm (DTW) in Luscinia. The DTW takes pairs of sounds of the same hierarchical level (phrase, song etc.) and divides each of them into 5 time series signals, evenly spread throughout the duration of the sound. Each time point is then characterised by the 5 acoustic features, with each feature weighted based upon the current best estimate for the saliency of change in that feature (Lachlan, in prep; Table 3.2). All acoustic features except time and normalised FF were normalised relative to the variance across the whole dataset. Normalised FF scores were normalised within the time-series signal itself, rather than across the dataset. The set compression factor meant that elements could not be reduced to less than 2 time points, and a maximum of 100% warp was utilised. Within syllables, elements were stitched together as long as the gap between them was less than 30ms.

Luscinia produces a dissimilarity matrix for each pair comparison, with one time series represented on the x-axis, and another time series on the y-axis. The DTW then searches for the optimal path (based upon minimising the Euclidean distance) in traversing this matrix from the first time-point to the last. The mean dissimilarity across this path is then calculated, resulting in a numerical score for dissimilarity between the pair. This is then repeated for all combinations of pairs within the dataset, resulting in the production of a dataset-wide pair dissimilarity matrix.

Table 3.2: Acoustic metrics and settings used in the DTW

Acoustic Metric	Weighting	Time Warp Setting	Value
Time	1	Compression Factor	0.2
Fundamental frequency	0.9	Maximum Warp	100%
Fundamental frequency change	0.86	Stitch threshold (ms)	30
Vibrato Amplitude	0.05	Cost of alignment error	0.2
Fundamental frequency norm	1.26		

3.2.3 Measuring vocal development

Recording sessions were grouped into individual-days as described in 2. To examine vocal development, songs of each individual were compared with each of the other songs that individual produced using DTW. Firstly, graphical representations of developmental change were generated by non-metric multidimensional scaling (NMDS hereafter) plots and were either colour coded based upon the date the unit was produced, or the relative timing of the unit in the song. To analyse change in phrase diversity over the time as well as sequential structure, a threshold-based match length entropy measure was utilised, as described in Chapter 2. Phrase entropy and phrase redundancy trajectories were then plotted for each individual.

Developmental trajectories in the yearling Tenerife chaffinches were placed alongside those of yearling *F.c.gengleri* for comparative analyses. Evidence found previously of reduced syntactical structure in *F.c.canariensis* compared to continental chaffinches, was further investigated through comparing the difference in redundancy in the last individual-day for each yearling, using a Wilcoxon rank-sum test. In *F.c.gengleri*, yearlings had crystallised a high redundancy song repertoire the last individual-day, and it was expected that *F.c.canariensis* redundancy would be lower overall at a comparable time period. In *F.teydea*, population-wide evidence suggests high precision in the learning of song-types (Lachlan, in prep), but prior to this study no evidence had been collected regarding the development of song. Therefore comparison of redundancy measures for the last individual-day were also made between *F.c.gengleri* and *F.teydea*, using a Wilcoxon rank-sum test.

For populations which produced yearlings with significantly lower redundancy than *F.c.gengleri*, we assessed the three outlined hypotheses (sluggish starters, early crystallisation and slow learning) for how the development of syntactical structure could have evolved. Evidence for the **sluggish starters hypothesis** in a population, was made through comparing the redundancy scores of individuals'

the first individual-day with *F.c.gengleri*. If the sluggish starters hypothesis was true, it would be expected that redundancy in the first individual-day to be significantly lower than *F.c.gengleri*. The mean recording date for these first individual-day was also compared, and where necessary, evidence of a reduced impact of seasonal time (day of the year) on the initial recording session was included.

The **early crystallisation** & **slow learning** hypotheses were assessed through three pieces of evidence. The first was the rate of gain in redundancy during an individuals' peak period of redundancy change which lasted greater than 14 days. The second was the time taken for an individual to go between 10% above minimum redundancy and within 5% of their maximum redundancy. The third was the day of the year at which individuals either reached within 95% of their maximum redundancy or the end of their peak development. These were compared between individuals in the target population and *F.c.gengleri* through the use of a Wilcoxon rank-sum test. If yearlings got within 95% of their maximum redundancy earlier or in significantly less time than *F.c.gengleri*, then it would provide evidence of **early crystallisation**. If yearlings take significantly longer to reach maximum redundancy, made lower redundancy gains during their peak developmental period, or achieve maximum redundancy at a later date, this would be considered evidence supporting **slow learning**.

3.2.4 Rhythm

To assess whether Canarian chaffinch species changed their rhythmic consistency over development like their continental cousins, each song for each developer had inter-onset intervals measured (the timespan between the onset of one syllable, χ and the following syllable, χ^{+1}. Each syllable was then time-stamped as the individual-day it was assigned and extracted into R. IOI times were then presented as phase-space plots (Ravignani, 2017), two dimensional scatter plots where the x-axis represents the IOI time between χ and χ^{+1}, and the y-axis the IOI time between χ^{+1} and χ^{+2}. Points within this scatter plot were then assessed for clustering tendency over time using the Hopkins statistic. For each individual-day, the dissimilarity to the k-nearest neighbour of points in the scatter plot is compared to 10000 randomly generated data drawn from a normal distribution. This produces a figure of clustering tendency for each individual-day calculated through mean k nearest neighbour distance for each individual-day, divided by the mean k-nearest neighbour from both real and all simulated data-sets. The output metric is between 0.5 and 1, where randomly distributed data would score 0.5 and clustered data trending towards 1. The impact of developmental time on

clustering tendency was tested through a LMM conducted using the lmer function in R (lme4). Two models were produced; a null model, and one which featured IOI individual-day as a fixed effect. Model fit was tested through the ANOVA function in lme4, and assessed by examining which scored the lowest AIC score, as well as if Model 2 had a significantly different log-likelihood ratio, as measured through a chi-squared test.

Table 3.3: Nested models for measuring IOI clustering tendency

Model	Description	
Null Model	Hopkins statistic of IOI clustering tendency	1 +(1|song)
Model 2	Hopkins statistic of IOI clustering tendency	date + (1|song)

3.2.5 Overproduction in *F.teydea*

To investigate whether the overproduction of songs was prevalent in *F.teydea*, we ran each developer through a DTW alongside songs taken from 65 adults recorded across Tenerife. The resulting song dissimilarity matrix was then exported into R, to search for examples of wild song-types that a developer learned but were removed from the repertoire. This involved a 3-stage process of narrowing down the possible options for overproduced songs. Firstly, all pairs of songs which had dissimilarity greater than 0.1 were removed, as scores above this threshold are not song-type matches. Secondly, all songs that scored less than 0.1 dissimilarity with the individuals own exemplar song-type were removed, as these cases would have been the song-type learned by the bird rather than overproduced (either produced by the bird or by a neighbour). For the songs that remained, songs were isolated which scored below a 0.075 threshold level of dissimilarity, with one produced by another individual. Each pair of songs in this subset had their spectrograms manually examined to confirm that these song-types matched, with the overall level of overproduction calculated based upon the number of song-types that passed this criterion vs the total number of songs produced by yearlings.

3.3 Results

3.3.1 Recording effort

3.3.1.1 *F.c.canariensis*

7 yearling common chaffinches were recorded for over at least 4 sessions of their vocal development (Table 3.4) and were taken forward for further analysis (Figure 3.3). Between the 22nd February and 10th March 2015, the Anaga National Park was surveyed each day, except for the 7th & 8th of March for which there was

substantial rain. Considering first visits to field sites only (to reduce the likelihood of double counting), observations of 351 adult chaffinches correlated to the finding of only 5 singing yearlings of which 2 form part of the final 7. The initial surveying strategy of using a combination of observation and playback proved only successful in invoking responses from older adults. One factor driving the greater use of playback detection was in the topography of the habitat surrounding the transects. The Anaga National Park is a montane laurel forest with roads and footpaths often surrounded by steep cliffs which made it difficult to approach birds by foot. Visual examination of yearling responses to playback demonstrated regular reticence to approach a speaker, and they often appeared oblivious to any stimuli played. This was especially noticeable at picnic sites, where yearling chaffinches fed regularly, but never sang. In total, a further 15 yearlings were recorded singing between 22nd February and 1st April for between 1 - 4 recording sessions. To combat the lack of initial yearling detection, a greater surveying area was assessed from the 11th March which incorporated more traversable habitats. This included lower altitude mixed forests of the Corona Forestal National Park, as well as agricultural land and agricultural-edge *barrancos* at the base of the Anaga National Park. Within these new habitat types, singing yearlings were encountered at a greater rate than previously.

The number of songs analysed for each of these individuals varied quite substantially (maximum = 486, minimum 184, mean 290.6 per individual). Whilst the lateness in which the bird was detected did play a role, individual differences in the reliability of song-bouts were equally important. Individuals such as JTench03 and JTench07 were fairly consistent in singing regularly throughout the morning and would also respond to playback when instigated. JTench01 and JTench16 proved more challenging, often only singing in a flighty 10-minute segment before sunrise and never responding to playback. Similarly, adult birds recorded in 2018 for both developmental comparisons and for later playback experiments (see Chapter 4) were also far more reticent to sing outside of the dawn chorus. Difficult lighting and terrain at these times made for challenging recording sessions, and therefore whilst the number of songs recorded might be quite high, the recording quality was regularly not of enough quality to analyse further.

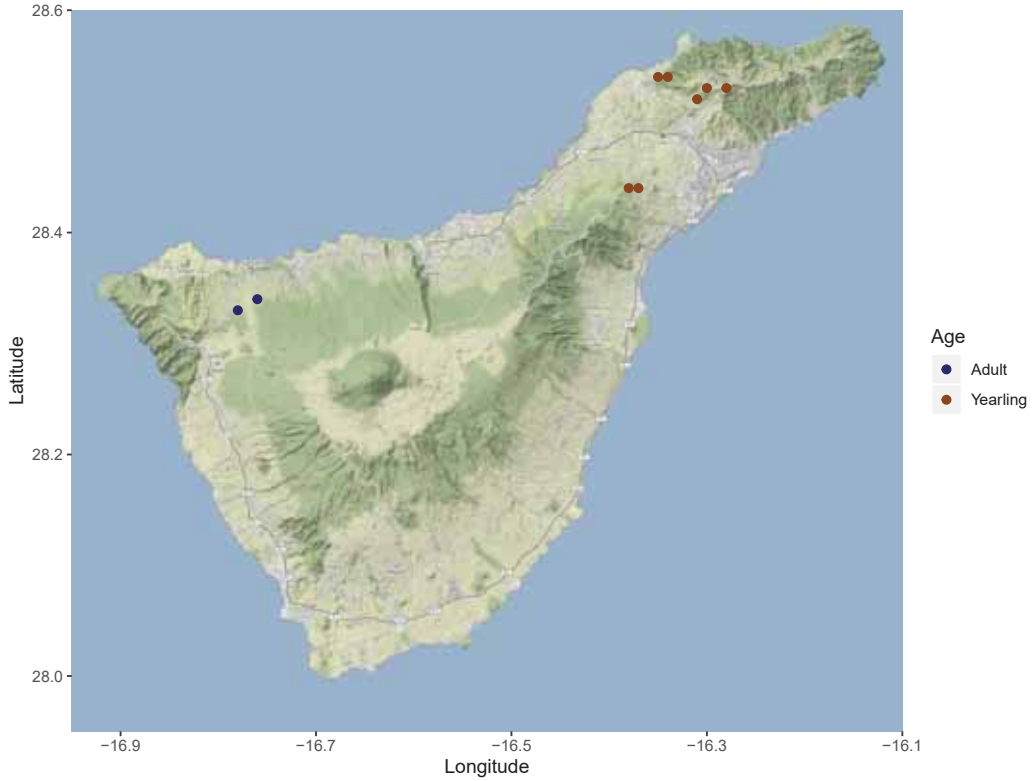


Figure 3.3: Distribution of territories of *F.c.canariensis* individuals recorded over development

3.3.1.2 *F.teydea*

7 vocally developing blue chaffinches were identified and recorded for greater than 5 sessions in Spring 2018 and were taken forward following further analysis (Table 3.5). Most birds were first sighted between 1st and 10th March which followed a spell of bad weather in region between (23rd - 28th February) where there were high winds and widespread flooding. Prior to this, singing blue chaffinches were present in breeding habitats, but not widespread, and all singing individuals were visually identified as adults. Two of the locations in which juveniles were later recorded were surveyed prior to the 1st March without detection of a territorial bird. This would suggest that these territories became occupied during this spell of bad weather. Following the discovery of the initial yearling on the 1st March, visits to new sites tended to result in yearling discovery.

Yearlings found were in two main areas (Figure 3.4). One was just north of Vilaflor in the south of the island, in a large expanse of Tenerife pine forest. 3 yearlings were located here, including 2 individuals near to the Paisaje Luna which shared a territory boundary. The territories were separated by a gravel track, which the birds were hesitant to cross even if playback was used on the opposite side. The

other area was Chinyero, on the western side of the island, close to the Montanas Negras. This habitat was patchier, with areas of Tenerife Pine recovering from historic volcanic eruptions. A further 4 yearlings were found here, and a nearby adult was also recorded for 5 sessions as a comparator.

Similarly with *F.coelebs*, the number of songs recorded for each individual were highly variable (maximum = 437, minimum=185, mean 296.875). Certain individuals, such as BY6 and BY2 would always respond vocally to playback, whilst others (BY3 & BY5 for example) required much more patience, and would often not sing, even when other neighbouring adults were.

In general though, the flatter, rocky terrain interspersed with Canarian pine that *F.teydea* occupied in these regions proved easier to collect recordings than those of *F.c.canariensis*. More widespread access to optimal recording points, easier movement opportunity between perching points, and less foliage affecting recording quality all contributed to this. *F.teydea* are also less shy than *F.c.canariensis*, continuing to sing even when in direct line of sight and within 2m of an observer.

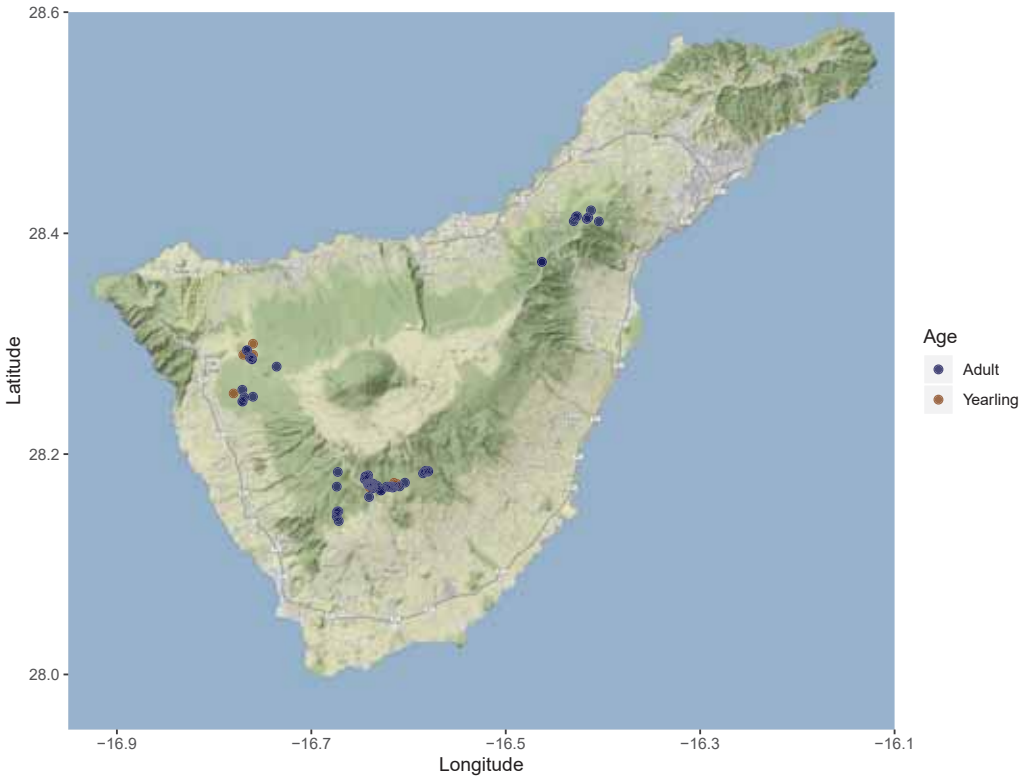


Figure 3.4: Distribution of territories of *F.teydea* individuals recorded over development, as well as adults recorded for the overproduction study

Table 3.4: Yearlings and adults of *F.c.canariensis* recorded for successive sessions between 2016-2018

Territory Latitude	Territory Longitude	Recordist	Age	Population	Name	First Recording	Last Recording	Songs Analysed	Individual Days
28.53	-16.28	JC	Y	Anaga	JTench15	22/02/2016	02/05/2016	486	11
28.54	-16.30	JC	Y	Anaga	JTench16	15/03/2016	26/04/2016	223	5
28.52	-16.31	JC	Y	Anaga	JTench13	24/03/2016	19/04/2016	215	4
28.54	-16.30	JC	Y	Anaga	JTench3	26/03/2016	22/04/2016	280	6
		JC	Y	La Esperansa	JTench01	11/03/2016	27/04/2016	184	4
28.53	-16.28	JC	Y	Anaga	JTench05	22/02/2016	01/04/2016	320	7
28.44	-16.38	JC	Y	La Esperansa	JTench07	27/03/2016	26/04/2016	323	6
28.33	-16.78	JC	A	La Montaneta	JATench1	24/02/2018	28/03/2018	192	4
28.34	-16.76	JC	A	La Montaneta	JATench2	24/02/2018	28/03/2018	118	3

Table 3.5: Yearlings and adults of *F.teydea* recorded during 2018

Territory Latitude	Territory Longitude	Recordist	Age	Population	Name	First Recording	Last Recording	Songs Analysed	Individual Days
28.29	-16.77	JC	Y	Chinyero	BCY1	15/03/2018	02/04/2018	227	4
28.17	-16.64	JC	Y	Vilaflor	BCY2	04/03/2018	01/04/2018	437	7
28.30	-16.76	JC	Y	Chinyero	BCY3	07/03/2018	30/03/2018	344	5
28.29	-16.76	JC	Y	Chinyero	BCY4	10/03/2018	02/04/2018	288	5
28.17	-16.61	JC	Y	Vilaflor	BCY5	01/03/2018	26/03/2018	328	5
28.17	-16.61	JC	Y	Vilaflor	BCY6	04/03/2018	29/03/2018	364	7
28.25	-16.77	JC	Y	Chinyero	BCY7	10/03/2018	31/03/2018	185	4
28.25	-16.77	JC	Y	Chinyero	BCA1	10/03/2018	31/03/2018	202	4

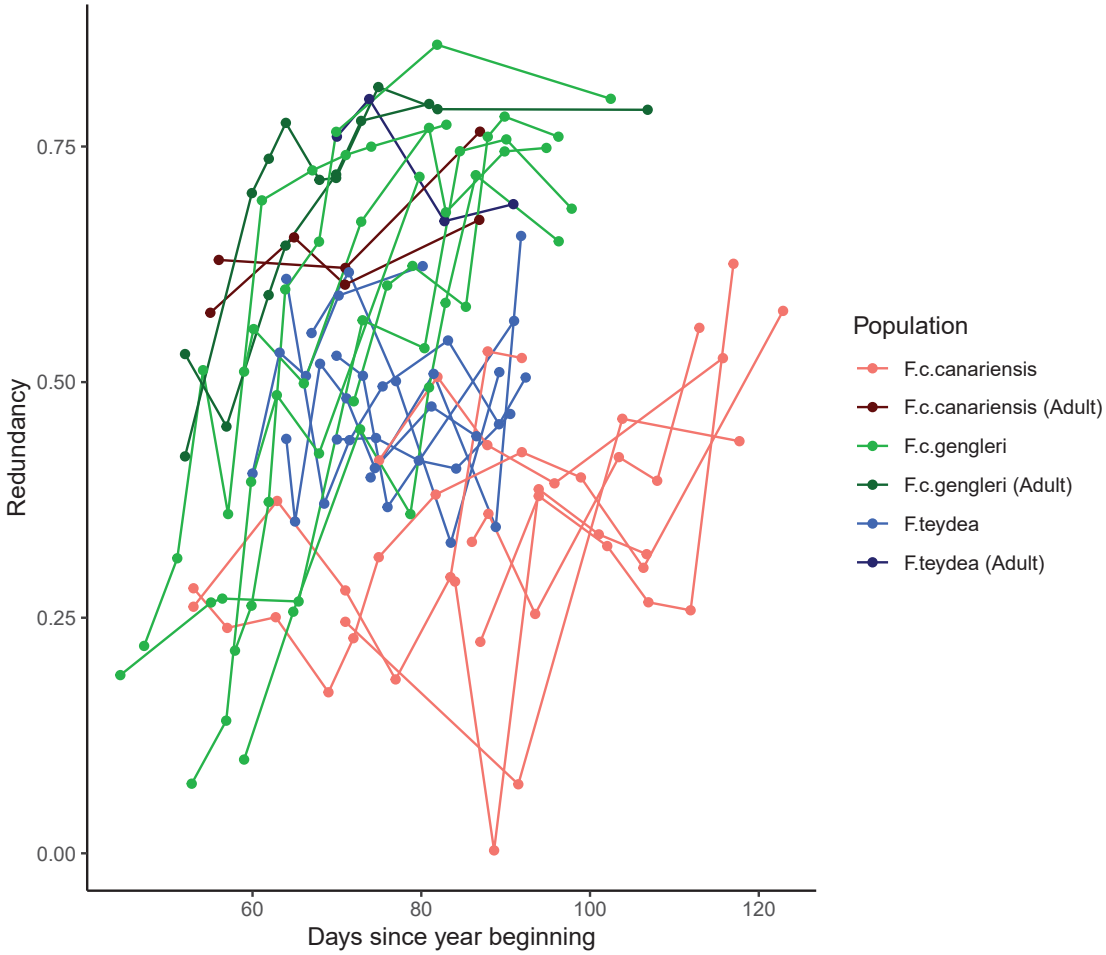


Figure 3.5: Trajectories of phrase redundancy over the development for yearlings and adults from 3 populations of chaffinches. Each point represents a calculation of normalised redundancy score for a given individual-day, where a score of 0 would represent that the individual produced songs constructed of phrases placed in a completely random order, and a score of 1 would indicate no randomness in phrase transitions.

3.3.1.3 Phrase sequencing over development compared with *F.c.gengleri*

The development of song sequence predictability (redundancy) was compared between the two Tenerife populations and the British population reported in Chapter 2. When comparing the redundancy scores of the latest individual day, those of yearling *F.c.gengleri* were significantly greater than those of *F.c.canariensis* (Mdn for *F.c.canariensis* 0.53, Mdn for *F.c.gengleri* 0.73, n = 7 ind. per pop., Wilcoxon rank-sum test. W=35, p<0.0001). This was also found to be the case for *F.teydea* yearlings (Mdn for *F.teydea* 0.51, Mdn for *F.c.gengleri* 0.73, n = 7 ind. per pop., Wilcoxon rank-sum test. W=48, p<0.01). Three potential hypotheses of changes that could occur during the development of sequencing phrases could result in these changes, shall be discussed in turn below:

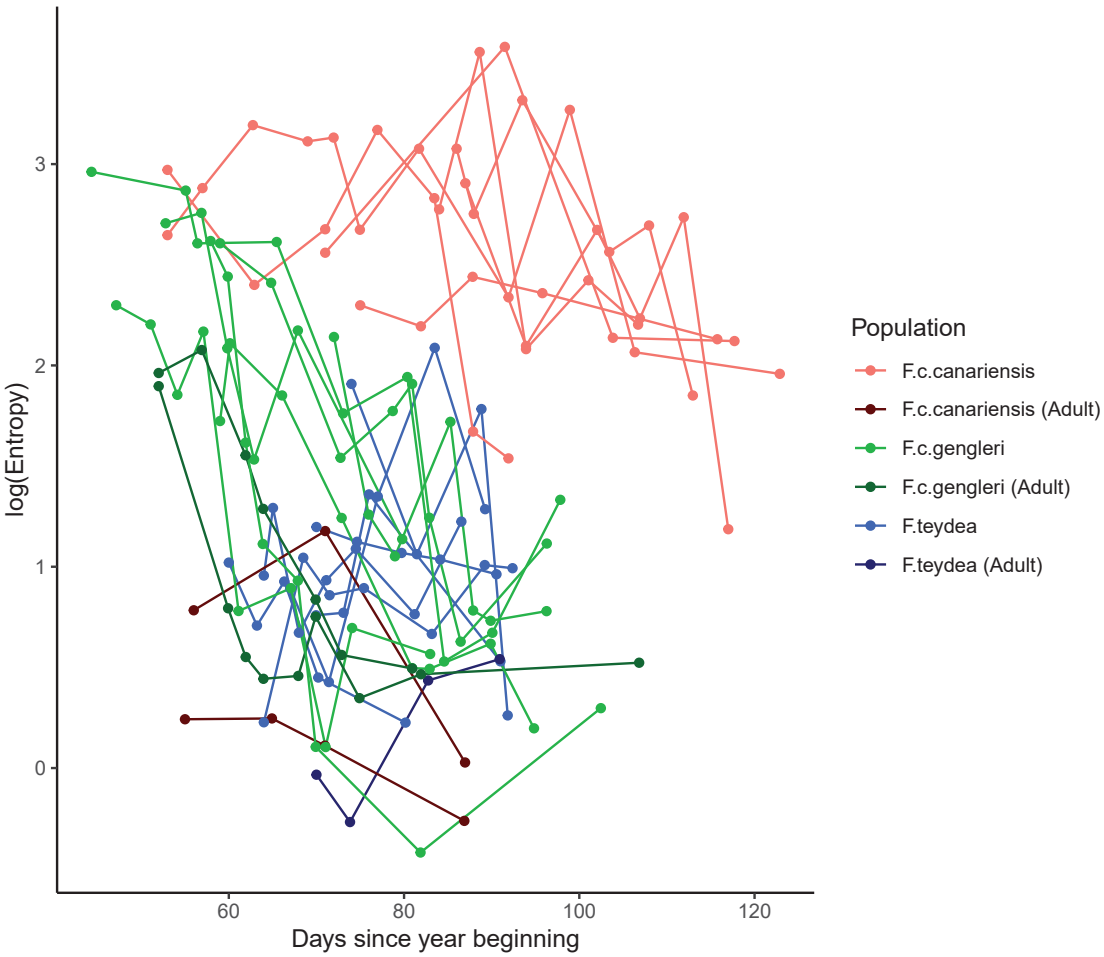


Figure 3.6: Trajectories for estimates of phrase diversity as reported through an entropy based measure, over the song development of yearlings and adults from three chaffinch populations. Lower scores indicate the use of fewer unique phrase types.

3.3.2 Hypothesis 1: Sluggish starters

3.3.2.1 *F.c.canariensis*

Firstly, I tested whether Tenerife yearlings began vocal development producing songs which were of lower redundancy than their British cousins. When comparing the first redundancy score between *F.c.canariensis* and *F.c.gengleri*, no significant differences were found in the redundancy scores between them (Mdn for *F.c.canariensis* 0.28, Mdn for *F.c.gengleri* 0.21, n = 7 ind. per pop. Wilcoxon rank-sum test. W=35, p=0.2). The mean year day for these measures was later in *F.c.canariensis* than in *F.c.gengleri* (day 73 compared with day 57), therefore it could be argued that if both populations were recorded at the same time point, then the redundancy for *F.c.canariensis* would have been lower. Two pieces of evidence suggest this might not be the case. Firstly, the 2 individuals first recorded between yearday 50-60 have comparable redundancy scores to the British birds recorded within the same 10-day period (Figure 3.5). Even individuals that did reach low redundancy scores, did so having been first recorded with redundancy levels comparable with British yearlings. As a second point of evidence, yearling chaffinches may begin defending a territory in Tenerife over a much broader timeframe than in Britain. Songs which are inconsistent in structure are seldom heard in Britain in late March, and almost never in April, as territory acquisition occurs in the last 2 weeks of February. In Tenerife however, 12 separate instances of yearlings producing subsong were recorded between April 1st and May 8th. As the production of subsong indicates these were yearlings and were either defending new territories or seeking to establish new ones, it seems likely that Tenerife yearlings are under less constraints to establish territories within such a restricted time window. With this in mind, it is reasonable to expect that yearlings would have a greater range of recording times in Tenerife compared to the UK. Therefore, the sluggish starters hypothesis is rejected for *F.c.canariensis*.

3.3.2.2 *F.teydea*

When comparing the first recording session of yearlings from *F.teydea* and *F.c.gengleri*, the songs produced by *F.teydea* had significantly higher redundancy (Mdn for *F.teydea* 0.43, Mdn for *F.c.gengleri* 0.21, n = 7 ind. per pop. Wilcoxon rank-sum test, W=8 p<0.04) (Figure 3.5). If the sluggish starters hypothesis were to be true, the redundancy scores of *F.c.gengleri* would be expected to be greater. As with *F.c.canariensis*, the mean year day for the first recording session was later for *F.teydea* than *F.c.gengleri* (day 66 compared to day 57). However, similarly to *F.c.canariensis* there is likely to be more relaxed time constraints behind the establishment of territories. Alongside this, redundancy values for *F.c.gengleri* in

the first dates recorded were comparable to *F.teydea* (Figure 3.5). As a result, the sluggish starters hypothesis is also rejected for *F.teydea*.

3.3.3 Hypotheses 2 & 3: Early crystallisation and Slow Learning

3.3.3.1 *F.c.canariensis*

The mean year-day by which *F.c.canariensis* yearlings reached 95% of their maximum recorded redundancy was year-day 102. This was a significantly later date than found in *F.c.gengleri* (Mdn year-day: *F.c.gengleri* 81.9, *F.c.canariensis* 103.8, n=7 ind. per pop., Wilcoxon rank-sum test, W = 45, p = 0.01). In 5 out of the 6 yearlings observed to pair with females during fieldwork, the first evidence of mate guarding behaviour in individuals was also found to occur prior to males reaching within 5% of maximum redundancy (mean year-day for mate-guarding behaviour 93, latest date 100). The rate of increase in redundancy during an individuals' peak period of development was significantly lower in *F.c.canariensis* compared with *F.c.gengleri* (Mdn redundancy gain *F.c.gengleri* 0.025 per day, *F.c.canariensis* 0.016 per day, n=7 ind. per pop., Wilcoxon rank-sum test, W=5, p<0.02, Figure 3.7). The day of the year for which the peak development ended was also significantly later in *F.c.canariensis* than *F.c.gengleri* (Mdn year-day: *F.c.gengleri* 81.9, *F.c.canariensis* 115.8, n=7 ind. per pop.,Wilcoxon rank-sum test, W = 49, p<0.001). The rate of increase between the lowest redundancy score and the time point to reach maximum redundancy was also significantly lower in *F.c.canariensis* than in *F.c.gengleri* (Mdn redundancy gain *F.c.gengleri* 0.021 per day, *F.c.canariensis* 0.008 per day, n=7 ind. per pop., Wilcoxon rank-sum test W=2, p<0.005, Figure 3.8). Based upon these findings, *F.c.canariensis* do not crystallise their songs earlier than *F.c.gengleri* and instead take longer to develop their songs, doing so at a slower rate. As a result, the slow learning hypothesis is accepted for *F.c.canariensis*.

3.3.3.2 *F.teydea*

The shorter overall time spent recording *F.teydea* compared to *F.c.canariensis* limited evidence of later breeding season (post-pairing) redundancy increases, which appear to occur given the disparity between the yearling and adult redundancy. As a result, no difference in the timing of development was found between *F.teydea* and *F.c.gengleri*. However, the rate of gain in redundancy during the peak period of development was found to be significantly lower than that of *F.c.gengleri* (Mdn redundancy gain *F.c.gengleri* 0.025 per day, *F.teydea* 0.011 per

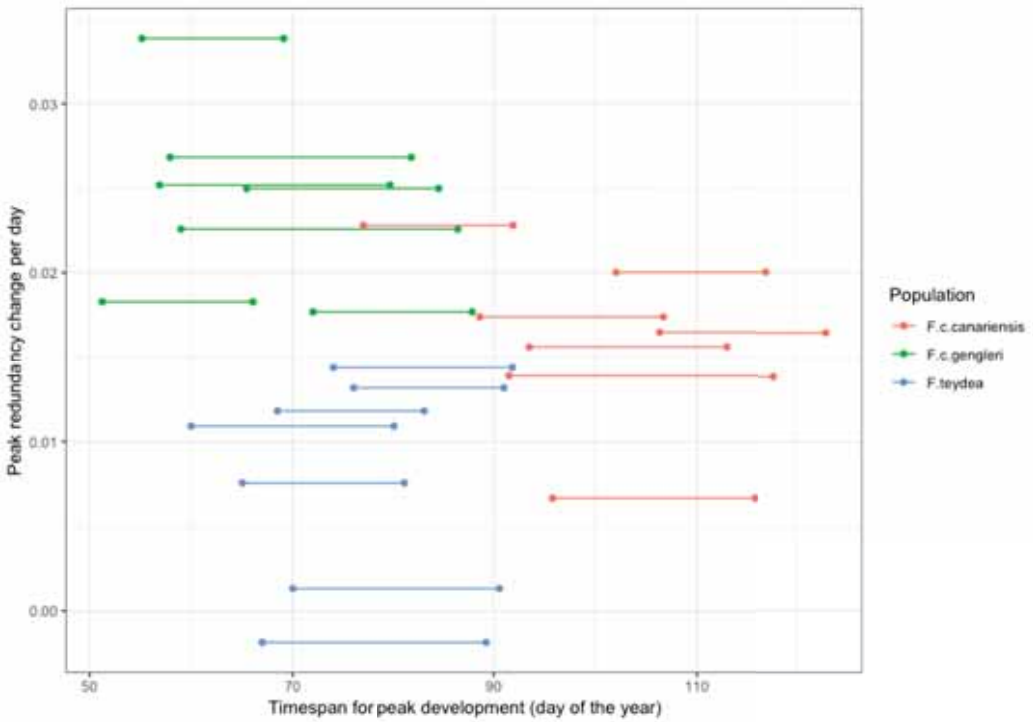


Figure 3.7: Time periods and rate of redundancy gain for the peak period of song development in 7 yearlings of three chaffinch populations. Each pair of points represents the start and end dates for the peak of development.

day, n=7 ind. per pop., Wilcoxon rank-sum test, W=49 $p<0.001$, Figure 3.7). The time taken to reach peak redundancy was marginally not significant between the two species (Mdn *F.c.gengleri* 19.12 days, Mdn *F.teydea* 17.83 days, n=7 ind. per pop., Wilcoxon rank-sum test, W=49 p=0.07). However, given that the birds had likely not reached the end of their development, findings may be liable to change if birds were recorded for longer. In this regard it seems acceptable to conclude that along with *F.c.canariensis*, *F.teydea* also develops over a longer sensorimotor period. The slow learning hypothesis is therefore also accepted for *F.teydea*.

3.3.4 Further notes regarding rates of redundancy development

One broader difference between the rate of development between these species is how concurrent phases of development occur in time. In *F.c.gengleri* we found that at the population level, the mean daily change in redundancy was greater than zero for all but one day between year-day 55 and 89 (Figure 3.9). For 7 dates between year-day 56 and 72, the mean - standard deviation of daily redundancy change was also greater than zero, indicating these are the dates for which peak vocal development occurred. In contrast, periods of consistent positive rates of

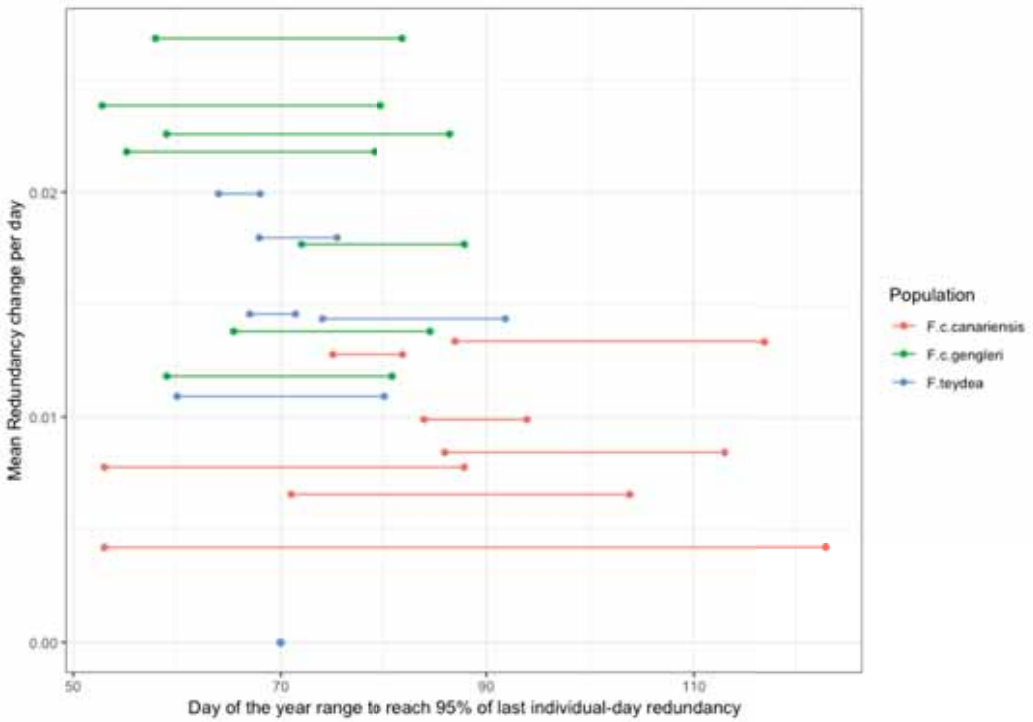


Figure 3.8: Time periods and rate of redundancy gain between the minimum and within 5% of the maximum redundancy achieved by 7 yearlings of three chaffinch populations. Each pair of points represents the start and end dates for the peak 14+ day period of development.

development were only found after day of the year 105 for *F.c.canariensis*. At no other point did either of the Tenerife chaffinch populations appear to have all individuals developing redundancy.

3.3.5 Development of Rhythm

3.3.5.1 *F.c.canariensis*

Change in the size and consistency of inter-onset intervals between syllables was assessed in the 7 yearling Tenerife chaffinches (Figure 3.10). For change in the size of inter-onset intervals, the inclusion of day of the year in our model did slightly lower the AIC score, but this difference was not a significant improvement over the null model (Chi-squared test 3.367, p = 0.065, df=1). The fixed effect estimate for day of the year was low (-0.0001) and negative, indicating that IOI times were generally becoming quicker as time progressed. One individual that does demonstrate this pattern is JTench3 (Figure 3.10b) where the quickest inter-onset intervals were all those it sang in the latter part of its song development. However, in the remaining birds, this pattern was not evident.

By contrast, when measuring inter-onset interval consistency, the inclusion of day

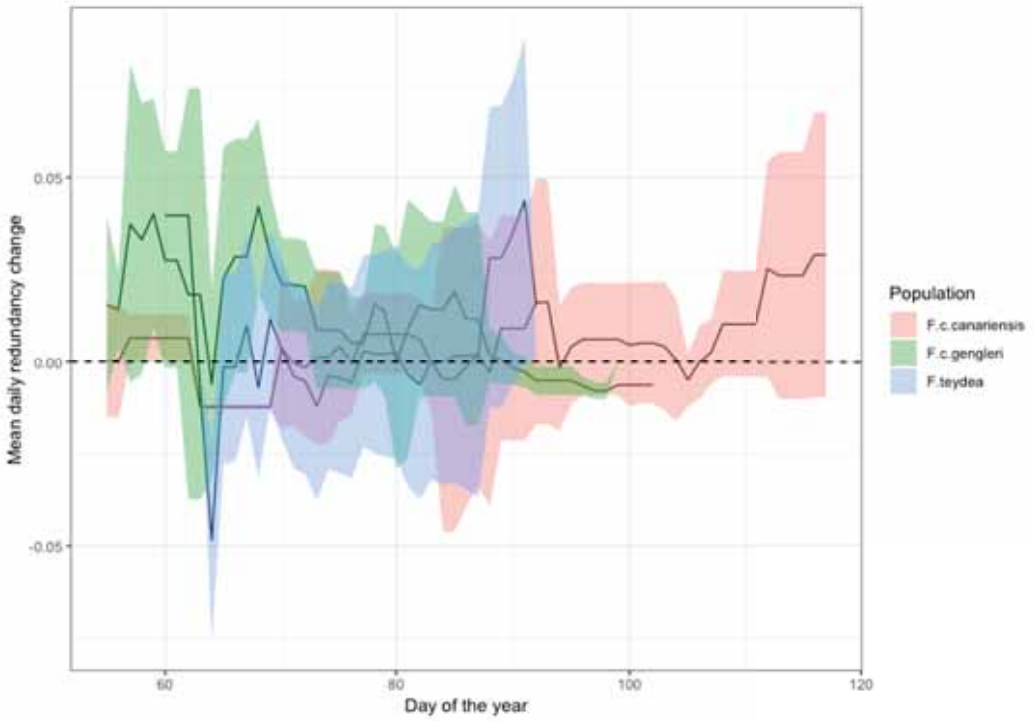


Figure 3.9: Rate of change in redundancy during song development per population. The mean redundancy change is represented by the line with the shaded border representing the upper and lower standard deviation of the mean.

Table 3.6: ANOVA summary comparing LMMs for change in rhythmic consistency in *F.c.canariensis*

Model Description:	df	AIC	Log-likelihood	χ^2	χ^2 df	P(χ^2)
IOI Clustering tendency 1 +(1|song)	3	-122.21	64.103			
IOI clustering tendency date + (1|song)	4	-131.28	69.642	11.08	1	<0.001

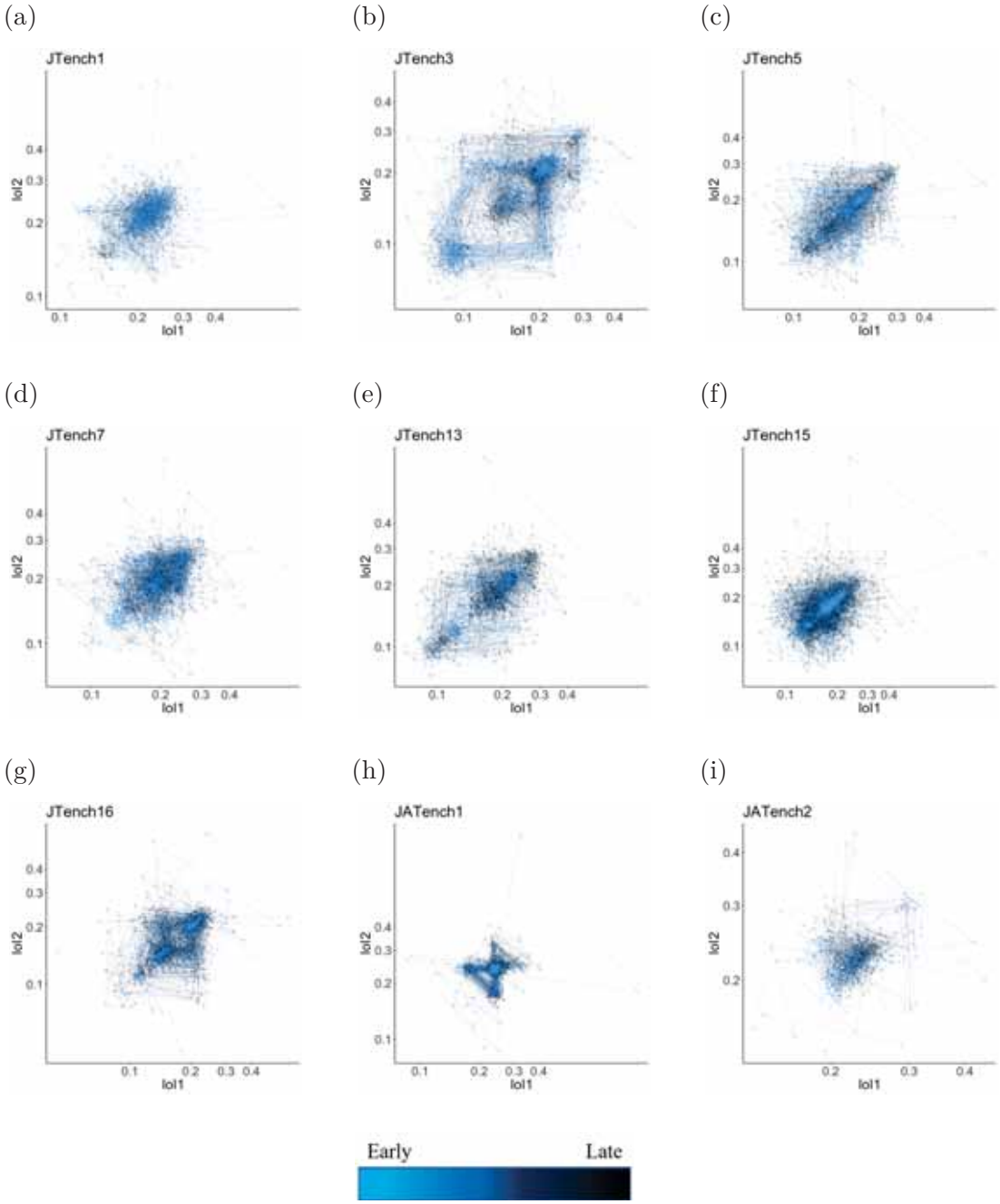


Figure 3.10: Phase space plots calculated on the IOI of syllable transitions for the 7 *F.c. canariensis* yearlings (a-g) and 2 adults (h-i) over time. The length of time between syllables for all songs for an individual are joined together as a sequence of IOIs (IOI1, IOI2., IOIn). Pairs of adjacent IOIs are then plotted on the x and y axes of a Cartesian plane. Lines in between each point represent the change in adjacent points. Points that fall along a 45-degree line (x=y) from origin represents pairs of syllables with equal IOI legnths, with clusters of these points inferring isochronous syllable production. Recording day is indicated with an individual blue colour scale, with darker points earlier recording sessions.

of the year was found to significantly improve the null model (Chi-squared test 11.727, p<0.0001, df=1). Over development, the clustering tendency of points on IOI phase space plots as calculated through the Hopkins statistic for each individual day (Figure 3.10), increased significantly. Across the developers, 5 out of the 7 birds show increases in the Hopkins statistic over time, as reflected in the density of lighter coloured phase space clusters (see Figure 3.10). These increases mirror those of sequence redundancy; a gradual increase from early in development, but at a lower rate than observed within *F.c.gengleri*.

3.3.5.2 *F.teydea*

The models which were applied to the *F.c.canariensis* dataset were then applied to the 7 yearlings in the *F.teydea* dataset. For change in the size of inter-onset intervals, the inclusion of day of the year was found to be a significant improvement on the null model (Chi-squared test 8.142, df = 1, p < 0.004). Unlike *F.c.canariensis* the fixed effect estimate for day of the year was positive (0.001), indicating that the rhythm of songs produced became slower as birds developed. This is perhaps most evident when examining IOI time change in BCY6 (Figure 3.11f).

On the other hand, change in clustering tendency of IOI times over development was not found to occur in *F.teydea* (Figure 3.11). The inclusion of day of the year did not improve the fit of the null model (Chi-squared test 0.8594, p = 0.35, df=1), and therefore the clustering tendency in the IOI phase space plots were not found to change over time. When compared to F.c.canariensis the clustering of IOI times had lower within-individual variation, but larger between-individual variation. Whilst no *F.c.canariensis* individual possessed rhythmic clustering levels close to adult birds, two F.teydea yearlings did across all of their recording sessions (Figure 3.12).

Table 3.7: ANOVA summary comparing LMMs for change in rhythmic consistency in *F.teydea*

Model Description:	df	AIC	Log-likelihood	χ^2	χ^2 df	P(χ^2)
IOI Clustering tendency 1 +(1|song)	3	-92.156	49.078			
IOI clustering tendency date + (1|song)	4	-91.015	49.508	0.89	1	<0.001

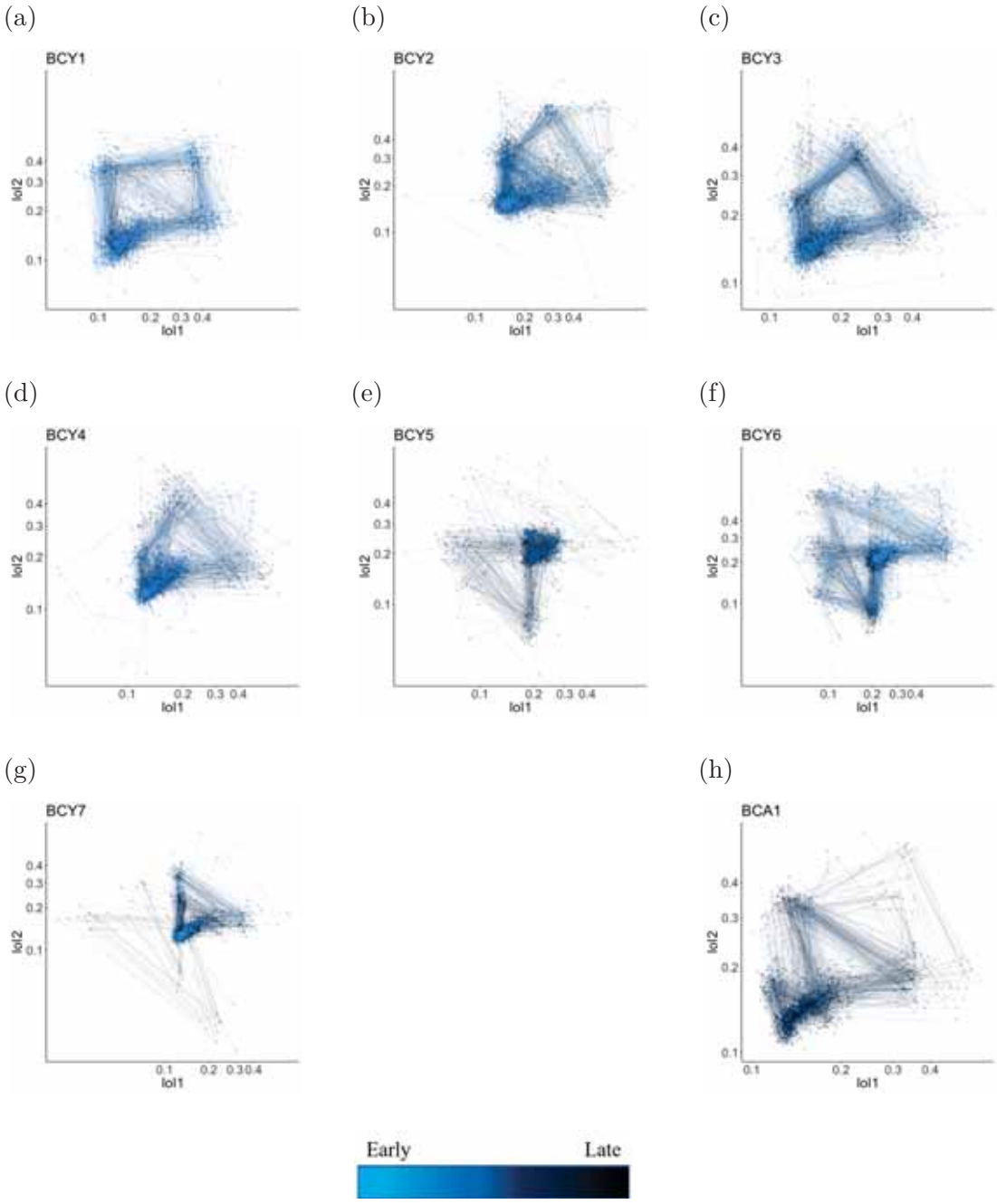


Figure 3.11: Phase space plots calculated on the IOI of syllable transitions for the 7 *F.teydea* yearlings (a-g) and 1 adult (h) over time.

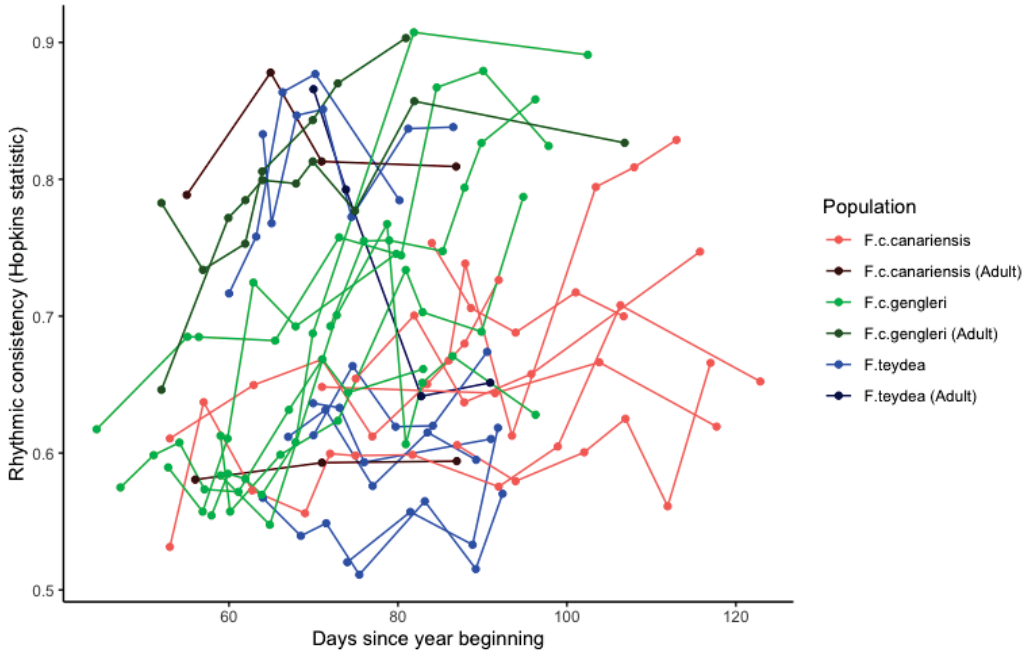


Figure 3.12: Trajectories for rhythmic consistency as measured through the Hopkins statistic on the phrase space plots over song development in 3 chaffinch populations.

3.3.6 Overproduction

Evidence for overproduction of neighbouring songs was examined in the 7 yearling blue chaffinches. 10 potential records of overproduced songs were detected (0.38% of total songs), all from a solitary individual (BCY5) and compared to a single song-type produced by BC06M. BC06M had been recorded the year prior to BCY5 and was recorded less than 200m from the eventual territory site of BCY5. All songs flagged as potential overproduced songs resembled a song-type which appeared intermediate between an exemplar of BCY5 and the song-type of BC06M (see Figure 3.13). These song-types all share a similar repeated syllable phrase and then a short syllable before a longer flourish. The dissimilarity score between the pair score 0.0103, fractionally above the threshold for which two songs could be considered the same song-type, but low enough for this to still remain a possibility. The lack of consistent phrase production even in the latest individual day for BCY5, may also mean that the exemplar selected from the song dendrogram may not have best represented songs belonging to the same song-type. Given the similarity between the BCY5 exemplar and the song-type possessed by BC06M, it remains inconclusive as to whether the songs flagged as being overproduced where poor imitations of the eventual exemplar, or genuine cases of overproduction. Coupled with the lack of overproduction found elsewhere in the other yearlings, signals that this behaviour is either rare or absent part of song development in Tenerife Blue Chaffinches.

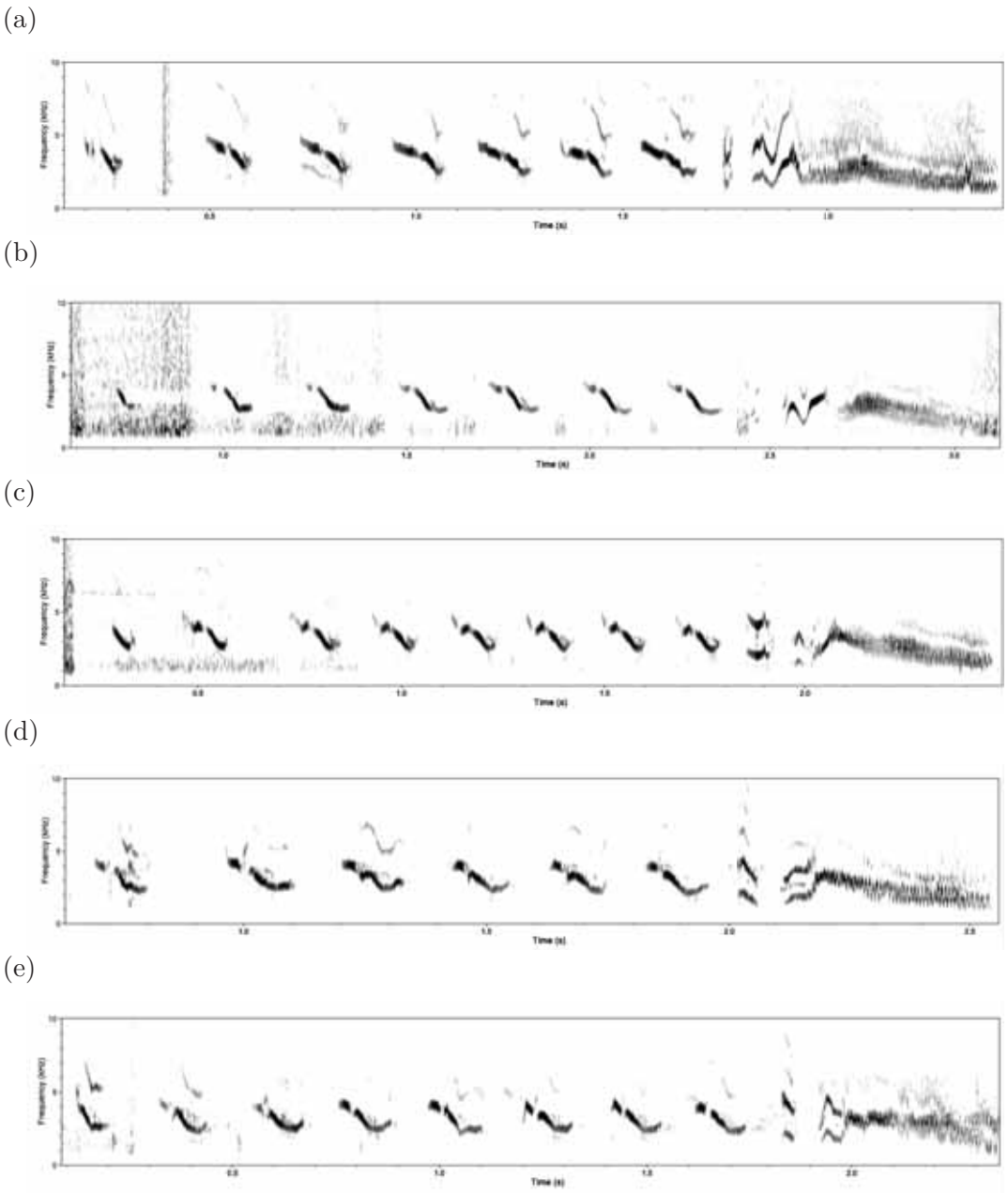


Figure 3.13: 5 *F.teydea* sonograms (Time 2.5-3.5s x-axis, Frequency 0-10kHz y-axis) which depict the only potential case of overproduction as identified through my analytical procedure. Spectogram a) is an exemplar from BCY5 not maintained in their adult repertoire b) is a song produced by nearby adult BC06M c) is a song produced by nearby adult BC10M, d & e) are two songs produced by BCY5 that were found to more closely resemble songs produced by other adults, than the exemplar for BCY5.

3.4 Discussion

3.4.1 Overview of the key findings

The primary finding from this comparative analysis of song development between three closely related populations of the genus *Fringilla*, was that the chaffinch populations on Tenerife, *F.c.canariensis* and *F.teydea*, acquire the syntactical structure of their songs slower than chaffinches from continental Europe. Though yearlings for all populations were detected singing in mid-late February (year-day 55 onwards) only individuals of *F.c.gengleri* reached the equivalent levels of sequential structure as found in adults of the species by the end of March (year-day 90). The peak time period of development also occurred significantly later in *F.c.canariensis* than it did in *F.c.gengleri*. This difference was also separated by mate selection, with Tenerife male chaffinches pairing with females prior to acquiring adult level sequential structure. For *F.teydea*, individuals failed to develop in sequential structure throughout the period of time spent recording them, and were still below the level of the recorded adult, as well as the typical level of sequential structure found in adults from the population (Lachlan, unpublished). Given this, and that recordings for *F.teydea* yearlings were conducted over a shorter period than *F.c.canariensis*, it seems likely they also undergo further sensorimotor development at a time-point after initial mate acquisition.

The findings above demonstrate a third major difference between the learning of song between chaffinches in mainland Europe, and those for a North Atlantic Islands. Previously, it had been uncovered that island birds mix and match syllables learnt from multiple tutors into their songs rather than retaining all phrases in the songs, such that they are no longer able to mimic song-types precisely (Lynch and Baker (1993), Lachlan unpublished). Also, Atlantic Island chaffinches had much more relaxed constraints on the sequential position of particular syllables than found in continental birds (Lachlan et al., 2013). Through this study, I add evidence of an elongated sensorimotor development in both *F.c.canariensis* and *F.teydea*, and a shift in peak timing for development in relation not only to day of the year, but also relative to key life history events such as mate acquisition, for which song quality may play an important role.

Although these methods demonstrate a much more detailed and quantitative way to analyse differences in song development, they are in agreement with comparative studies of other closely related taxa. In the white-crowned sparrows, the *Z.l.gambelii* developed songs much more quickly than other subspecies (Nelson,

1999; Nelson et al., 1995). Furthermore, despite spending significantly longer producing plastic song, *Z.l.oriantha* produced less precise imitations of tutor syllables than *Z.l.nuttalli*. Between these two species, we therefore make the suggestion that slower rates of song development may be more broadly linked to less accurate learning.

Hughes, Nowicki, Searcy, and Peters (1998) argued that the differences in song sharing between sedentary and migratory populations of song sparrow were linked to observable differences in how individuals from those populations acquired songs; with a sedentary population from Washington learning song types fully, and the migratory Pennsylvania populations mixing and recombining song segments, in a similar vein to the *F.c.canariensis*. It would therefore also be interesting to see if similar patterns of song development observed in the Atlantic Islands chaffinches were also found in the song sparrows.

Another species which could be readily compared with the chaffinch is the Atlantic Canary *Serinus canaria*. This finch species lives exclusively in Macaronesia, but is globally widespread as a domesticated species *Serinus canaria* forma *domestica*. The canary is an open-ended song learner, increasing the number of syllables in its repetoire as it gets older (Güttinger, 1985; Nottebohm & Nottebohm, 1978b; Nottebohm, Nottebohm, Crane, & Wingfield, 1987). Studies comparing wild and domestic canaries found that domesticated canaries possess a smaller syllable repetoire than their wild counterparts, and also tend to repeat syllables more frequently (Voigt, Leitner, & Gahr, 2001). However, the levels of increase in syllable repetoire in relation to age are comparable with that of wild birds (Voigt et al., 2001).The rate of song development has been investigated in the domestic strain in relation to hatching time (Leitner, Teichel, Ter Maat, & Voigt, 2015). Leitner et al. (2015) found that though late-hatching males were worse in physical condition as adults, no differences could be found between their songs and those of males which hatched between 50-90 days before. The authors concluded that canaries which hatched later had accelerated the process of song development. With the chaffinches in mind, it could be argued that rather than the Canarian birds being slow to learn, the environmental conditions in temperate Europe necessitate accelerated development. This could be investigated by running a comparible developmental assessment with the migratory Scandinavian chaffinch population, where egg-laying can be nearly a month later than in *F.c.gengleri* (B. W. Svensson, 1978).

In the Brown-headed cowbird *Molothrus ater* yearlings were also found to display substantial variation in the time required to produce “adult-like” vocalisations

(O'Loghlen & Rothstein, 1993, 1995, 2002). Some yearlings take a solitary breeding season to learn an equivalent repertoire to adults, whilst others take multiple breeding seasons (O'Loghlen & Rothstein, 1993, 1995). Given that the timing of yearling subsong was found to be more variable in *F.c.canariensis*, it would be interesting to examine whether similarly large variation in the time to produce adult songs was found.

In *M.ater*, field evidence initially indicated that individuals residing in higher altitudes, rather than belonging to a particular population or subspecies, had a much higher proportion of elongated vocal development (O'Loghlen & Rothstein, 1993, 1995, 2002). However, later assessment of development from individuals taken from low-altitude habitats to be raised in the laboratory revealed similarly low development in this population (O'Loghlen & Rothstein, 2002). The authors argued that comparing field evidence of differences between adults and yearlings may not represent the performance of all yearlings in the population. For example, in two populations for which one had greatly more available territories than another, and for which territory acquisition was more successful in fast-learning than slow-learning individuals, one could observe far lower rates of slow-learning simply due to slow-learners being unable to defend a territory. Whilst it might be the case that lower quality chaffinches from the continent might develop songs equivalent redundancy to Tenerife populations, but be unable to hold a territory in a saturated environment, given the breadth of habitats in which chaffinches breed on the continent, and the consistency for which it has been recorded learning precisely, it seems highly unlikely that it would explain the variation between the continent and all of the Atlantic Island chaffinches.

Taking this into consideration, what other factors could have resulted in this re-engineering of development in the islands chaffinches? Migration was a key factor attributed to the changes in development found within several subspecies of *Z.leucophrys* as well as *M.melodia* (Hughes et al., 1998; Nelson, 1999; Nelson et al., 1995). Migration in the Atlantic Island chaffinches is also low, with extremely few reports of any individuals migrating across the Canary Islands (Garcia-del-rey pers. comm). Some continental chaffinches, particularly those which breed in Northern and Eastern Europe, are highly migratory. However, in a large proportion of the European and British chaffinch population, migration and juvenile dispersal are also extremely low (Paradis, Baillie, Sutherland, & Gregory, 1998) and comparable to what is expected to occur in the Atlantic islands. It is therefore unlikely that migration plays a role in the evolution of development found in the chaffinches.

One obvious area to consider would be the differences between island and mainland

ecology. It has been suggested that as a consequence of lower genetic diversity (Griffith et al., 1999), increased territoriality and/or brood investment (Covas, 2011), sexual selection may be less intense in island populations. For females, distinction between precisely learnt and less precisely learnt song may no longer carry sufficient fitness benefits as it does on the mainland, and as a result, males need no longer need to invest in developing songs as precisely. It can be argued that similar patterns to these, have been artificially created in the white-backed munia *Lonchura striata*. In the wild, individuals develop a highly stereotyped song, much like the continental chaffinch (Honda & Okanoya, 1999; Takahasi & Okanoya, 2010). However, the domesticated strain of the species the Bengalese finch (*L.s.domestica*), instead develops songs of low redundancy, with one syllable able to transition into multiple others (Clayton, 1987; Okanoya, 2004; Okanoya & Yamaguchi, 1997). Through comparisons between the two strains, it has been found that female preferences for complex songs were linked to domesticated environments (Okanoya, 2017). These environments, characterised by features such as low genetic diversity, high offspring survival, low predation, low heterospecific competition, low food competition, low temperature variance & low levels of migration are also shared with island ecology (Honda & Okanoya, 1999; Losos & Ricklefs, 2009; MacArthur et al., 1972; Whittaker & Fernández-Palacios, 2007).

However, when examining the genetic diversity of all chaffinch populations in the Canary Islands, only those El Hierro were found to have been subject to a strong genetic bottleneck (A. J. Baker et al., 1990). No evidence of genetic bottleneck effects was reported in either the Tenerife blue chaffinch or the Tenerife common chaffinch. Therefore, females should still remain able to select males for which they would have a higher genetic fitness, and males able to signal this through song. Nevertheless other factors besides genetic changes may have reduced sexual selection resulting in a reduced benefit of learning songs precisely and quickly.

The findings reported in this study of elongated development also appear at odds with the idea of reduced investment in song development. During the sensorimotor phase, a bird maintains high levels of hormones, such as testosterone (Marler, Peters, Ball, Dufty Jr, & Wingfield, 1988) to instigate song production, which involves complex muscular contractions that also carry a significant metabolic cost (Oberweger & Goller, 2001; Thomas, 1999, 2002). In addition to this, a developer must express behaviour-driven genes which facilitates the neurogenesis that gradually reduces the plasticity of song units produced by the bird (Arnold, 1992; Kirn, 2010; Nottebohm, 1992). As a result, it would be expected that a lengthening of the sensorimotor phase of song development would incur a higher energetic cost than a shorter phase. But in a situation where selection of a learned

trait was weaker, it would be predicted that individuals would invest less resources into its development, rather than more.

One possibility is therefore that whilst the birds take longer to reach adult-equivalent levels of song learning, investment into song development occurs over longer periods with lower physiological investment. In many species, the use of song changes with age (Gil, Cobb, & Slater, 2001; Nemeth, Kempenaers, Matessi, & Brumm, 2012; Nol & Smith, 1987; Nottebohm & Nottebohm, 1978a). In this scenario, the Tenerife chaffinches would simply invest into the creation of hormones that assist sensorimotor learning periodically. Based on the analysis of this study a potential late developmental period for *F.c.canariensis* could occur in late April to early May.

Alternatively, evidence from other songbird species has demonstrated that their sensorimotor development took longer, when under greater nutritional stress. Nowicki, Searcy, and Peters (2002a) found that by restricting food, hand-reared swamp sparrows would spend longer producing subsong and plastic song, as well as entering subsong stage earlier. In addition, developmentally stressed zebra finches have been found to have reduced accuracy in how they acquire song syntax (Boogert, Lachlan, Spencer, Templeton, & Farine, 2018; Brumm, Zollinger, & Slater, 2009; Holveck et al., 2008). One possible explanation for slow learning is that the ecological conditions of Tenerife produce a broadly more stressful environment to learn songs than across the rest of their range on mainland Europe, which in turn elongates the time taken for sensorimotor development.

However, this is unlikely to be the case. Firstly, the developmentally stressed individuals in Nowicki, Searcy, and Peters (2002a) retain the same time-point for crystallisation as control birds, despite spending longer in phases prior to this. To my knowledge, no other investigation examining developmental stress has reported a lengthening of the point of crystallisation in developmental stressed birds. Secondly, chaffinches occupy a range of habitats in the Atlantic Islands. Whilst in Tenerife, chaffinches are fairly restricted to montane laurel forests and scrub, in the more northerly Azores, chaffinch habitat includes arable farmland, broad-leaf woodland and recreational parks and gardens. All of the Azorean habitats are fairly typical of those occupied by chaffinches in continental Europe. Of course, it might be the case that slow learning is exclusive to Tenerife or particular conditions experienced by chaffinches on Tenerife that might be absent on other Atlantic Islands.

Lachlan et al. (2013) argued that factors such as interspecific confusion were

unlikely to explain the changes in song learning found in the island's chaffinches, as although each island is less speciose than the mainland, those with the smallest number of non-corvid songbirds had the highest syntactical structure. Instead, Lachlan et al. (2013) linked their findings and those of (Lynch & Baker, 1993, 1994) to colonisation events. They reported that in song learning in *F.coelebs* became less like continental birds after each suspected colonisation event they made (Suárez et al., 2009).They hypothesised that as a result of cultural bottlenecks (a relative lack of song models available to yearlings) following each colonisation event, unusual song learning biases could escalate. An alternative theory presented by Lachlan et al. (2013) was that a lack of access to song models for females under conditions of high drift, could lead to relaxed learning biases under the cultural trap hypothesis (Lachlan & Feldman, 2003; Lachlan & Slater, 1999). However, linking cultural bottlenecks to a slowing of development has thus far proven challenging.

For a final potential explanation for slow learning that relates to the sensorimotor development studied here, a change in the underlying reinforcement provided by auditory feedback could also result in the song learning patterns uncovered here, and in previous studies. As a principle of reinforcement learning, listening to the bird's vocal output triggers neurogenesis during the plastic phase of song development. Neurogenesis is thought to be triggered by the resemblance between the songs a developer has produced and the memorised song model. However, this would not explain why adult Tenerife chaffinches learn songs of high redundancy for song models they had probably never heard in the wild. One way this could occur is if the bird's memory of a song was altered by the songs it had previously sung. Through this, a plastic production a song-type utilising phrases from multiple tutors could plausibly end up "fixing" a new song-type, whilst weaker levels of reinforcement may result in a lengthening of the sensorimotor phase. This notion that changing the sensitivity of birds to their own song output and how this could impact reinforcement learning, could be explored further through the creation of a developmental model.

3.4.2 Rhythm develops across *F.coelebs* populations

One feature from this study for which both subspecies of *F.coelebs* differ from *F.teydea* was in the development of rhythm. *F.c.canariensis* demonstrated a significant increase in the clustering tendency of the timings which separated the onset of syllable production in their songs. Rhythmic consistency of *F.teydea* was not to develop, much like reports from zebra finches *Taeniopygia guttata* (Aronov, Veit, Goldberg, & Fee, 2011; Bruno & Tchernichovski, 2017). Therefore, unlike in sequential redundancy, the populations which were closest related behaved

most similarly, rather than those which were the most ecologically similar. If the results for the presence of development in rhythmic consistency are considered alongside change in repertoire size, relaxed syntactical structure and an elongated sensorimotor development, then from an evolutionary standpoint, rhythm could be considered influenced under different mechanisms. The similarity between the trajectories for rhythmic development and sequential redundancy between the two *F.coelebs* populations were quite similar. For a better understanding of whether the differences in rhythmic development are additional markers which separate the two *F.c.coelebs* subspecies, further testing of other subspecies would be beneficial. Alternatively, it would also be highly interesting to run a comparative study tracing the development of both syntactical structure and rhythm in wild *Lonchura striata*. Both the development of sequential structure and rhythmic consistency have been measured in *L.s.domestica* (Okanoya, 2013; Sasahara et al., 2015) and as already discussed these two subspecies share similar song learning differences to the island and mainland chaffinches. Uncovering whether precise learning of syllables and syllable transitions also coincided with increased rhythmic consistency, would help provide new links between the relatedness of different song components and how they can evolve.

3.4.3 Overproduction not present in *F.teydea*

It had been previously suggested that one possible function for overproduction would be to enable males to match the song-types of territorial neighbours (Nelson, 1992b) with recent calls to increase the number of field studies exploring the behaviour (Peters & Nowicki, 2017). Here I report that in *F.teydea*, a species which displays high neighbour song-type sharing (Lachlan, in prep), there is little/no evidence of overproduction and selective attrition of song material. Based on the percentage of overall songs recorded, the level was lower than that of the British chaffinches in Chapter 2, which themselves were among the lower rates of overproduction when compared with numerous North American sparrow species. This could provide further indication that overproduction and selective attrition is not a widespread behaviour present across all songbirds. It could be argued that as the full scope of song development in *F.teydea* was not captured in this study, and that selective attrition might occur at time points not captured here. A point to make here would be that whilst redundancy in the *F.teydea* yearlings was lower in adults, the number of song-types learnt was similar (Lachlan, in prep). Therefore, both selective attrition and overproduction would need to occur prior to data collection for this study (with field-sites surveyed from year-day 48 onwards). Collection of further data regarding the singing behaviour of blue chaffinches,

particular in relation to potential autumnal or winter territory acquisition by juveniles, would be a key next step in exploring this possibility.

3.5 Conclusion

In summary, here I performed the first comparison of developmental trajectories in wild birds, based purely on computational assessment of songs produced. The main finding was that both *F.c.canariensis* and *F.teydea*, which are natural colonists of the Canary Islands acquire the syntactical structure of their songs slower than chaffinches from continental Europe. The completion of song development appears to occur much later, certainly after mate acquisition and possibly even during subsequent breeding seasons. Alongside, reduced precision of learning (Lynch & Baker, 1994), and lower syntactical structure (Lachlan et al., 2013), this is the third key song learning change found in the Atlantic Islands chaffinches. The nature of what has caused these changes continues to be unclear. However, through the discovery of slower and elongated developmental trajectories in the island's chaffinches can be used to improve our understand for conditions under which song evolves, and potentially earmarks changes in self-perception of auditory feedback during sensorimotor learning to these conditions.

Chapter 4

Evolution of female singing, duetting and territoriality in the Atlantic Island chaffinches

Abstract

The presence of female singing in a species appears to be mediated by both evolutionary history and ecological conditions. Previous work has highlighted the phylogenetic signal in female song, with female singing found to be prevalent across ancient clades of oscines. An alternative approach to this is to examine the evolution of female song in closely related taxa that differ in ecological conditions, though such studies are rare. Here, females of two chaffinch species *Fringilla coelebs* and *F.teydea*, which had previously been considered not to sing, are revealed to have independently started to produce song in isolated populations in the Atlantic Islands. Song recordings were analysed to isolate identifiable acoustic features of the songs and infer the degree of individuality and rates of inter-sex song learning. Females in both species sang much less than males, producing sex-specific songs without evidence of song-type sharing. In *F.coelebs*, the finding is the fourth major difference in song learning behaviour found between subspecies on the Atlantic Islands and those from continental Europe. In *F.teydea*, songs by females are produced in a "loose duet", overlapping with the ending of a male song. Following these observations, the function of female songs was assessed through a series of playback studies. Female songs from both species incurred significantly greater responses from territorial birds than an unheard heterospecific song. In *F.coelebs* male song tended to incur a greater territorial response than female song, though in some trials this was reversed. In *F.teydea*, territorial responses to song

were similar, even if stimuli were presented in a duet. The additional finding of extended territorial ownership in the Atlantic Islands, combined with the results from the playback studies is consistent with female song functioning in territorial conflicts. Future studies could use the discovery of female singing *Fringilla* in the Atlantic Islands to answer a broad range of outstanding questions regarding the development, evolution and function of female song.

4.1 Introduction

All songbird species studied to date have males which learn to produce song, but this is not the case for females (Hall & Langmore, 2017; Odom et al., 2014; Riebel, 2003). This is despite female singing being ancestral to the songbird linage (Odom et al., 2014). The presence of female singing for a given species, appears to be dependent on a combination of evolutionary history and environmental conditions, particularly those which promote year-round territoriality (Langmore, 1998; Odom et al., 2014, 2015; J. J. Price et al., 2009; Riebel, 2003; Slater & Mann, 2004). As a result, the diversity in the evolution of elaborate vocal signalling could be considered to be better examined in female songbirds than in males (Riebel et al., 2005). Previous studies which examine this relationship tend to focus either on the function of female song within a single species (Arcese et al., 1988; Baptista, Trail, DeWolfe, & Morton, 1993; Hall, Rittenbach, & Vehrencamp, 2015; Hobson & Sealy, 1990; Kriner & Schwabl, 1991; Langmore, Davies, Hatchwell, & Hartley, 1996; Matthews, Slevin, Worm, & Boves, 2017) or identifying broader ecological conditions through which a clade, or clades of female singers operate (Odom et al., 2015; J. J. Price et al., 2009). Rarely have such approaches combined to highlight specific conditions in which female singing has evolved, and the function they possess.

One reason for this is that female singing species are more common in the tropics (Odom et al., 2014; J. J. Price et al., 2009), where species life-history patterns are generally less-well understood (Slater & Mann, 2004). This link between the tropics and female singing is thought to be potentially due to a number of ecological factors such as increased resource availability, more consistent resource availability, smaller clutch sizes, low migration, longer territory ownership, and greater rates of monogamy (?, ?; Langmore, 1998; Slater & Mann, 2004). Female song has histroically been rarely reported in temperate species, and in cases where females did sing, it was often not linked to breeding behaviour, such as the winter song of female European robins *Erithacus rubecula* (Kriner & Schwabl, 1991). The previously long-standing textbook case for female singing, was that it was a

by-product of elevated androgen levels (Catchpole and Slater 1995 - NOIG).

Through more detailed studies, female song has since been found to have a broad range of functions across many species, including territory defence (Arcese, 1987; Arcese et al., 1988; Baptista et al., 1993; Cooney & Cockburn, 1995; Grafe & Bitz, 2004), mate acquisition (Langmore et al., 1996; Matthews et al., 2017) group defence (Seddon & Tobias, 2005), mate guarding (Seddon & Tobias, 2005), mate communication (Hall et al., 2015) and intrasexual contests (Arcese et al., 1988; Pavlova, Pinxten, & Eens, 2007). In some species, females also sing synchronously or alternately alongside their partner in a duet. Duetting is thought to have arisen through increasing the effectiveness of signalling when compared to a sole individual when competing with conspecifics for resources. Alternatively it could possess no combinational function, such as in mate signalling (Langmore, 1998; Levin, 1996).

For a given species, understanding the function of female singing can often be revealed through the timing of singing and responses of individuals when presented the song through speaker playback. Through a combination of examining song production and studying male responses to female song, Langmore et al. (1996) found female alpine accentors *Prunella collaris* would sing more when the likelihood of copulation increased and that males would treat female songs differently to males. Similarly, Hall et al. (2015) used a combination of recordings and playbacks to infer that the rare female song of *Thryophilus pleuroisticus* would not be directed towards territorial invaders, but instead would be coordinated with their breeding partner. Various methods have now been established for understanding the functions of female song, but no study can relate how these adaptations appeared in relation to differing ecology.

The European chaffinch *F.coelebs* has been historically prominent model species for male song learning, and the impact of song in territorial interactions and female song preferences (Lachlan & Slater, 2003; Marler, 1956a; Nottebohm, 1968; Riebel et al., 2015; Slater, 1981; Thorpe, 1954). *F.coelebs* males are highly territorial during the breeding season, regularly engaging an invading individual in either vocal or physical contests (Leitão & Riebel, 2003; Slater, 1981). Female singing has not been recorded in European populations of *F.coelebs*, (del Hoyo et al., 2011; Kling & Stevenson-Hinde, 1977), apart from a small number of anecdotal fieldnotes (Halliday, 1948; Lack, 1943; Marjakangas, 1981; Marler, 1956a; Warburg, 1941). Given the chaffinch is one of Europe's most abundant songbirds that regularly occurs in urban habitats, this indicates that singing in female chaffinches is extremely scarce in the wild. Kling and Stevenson-Hinde

(1977) injected females with testosterone and found the produced songs no different in structure to male counterparts on their first Spring. This therefore indicated that female chaffinches retained the capacity to be able to memorise songs of those around them and use them to guide auditory feedback to learn songs precisely.

Alongside the European populations of *F.coelebs* live several genetically isolated populations in the Atlantic Islands. On Tenerife there are two species of *Fringilla*, the Tenerife common chaffinch *F.c.canariesnsis* and the Tenerife blue chaffinch *Fringilla teydea*. Both species arrived on the islands as products of colonisation events from ancestral populations of neighbouring continental Europe and Africa (Marshall & Baker, 1999), respectively. *F.teydea* is endemic to Tenerife (Lifjeld et al., 2016; Sangster et al., 2016) and derives from the earliest colonisation c. 2mya (Rando et al., 2010). mtDNA analysis suggests *F.coelebs* colonised the islands more recently and sequentially; first colonising the Azores, then moving to Madeira, and lastly arriving on some of the Canary Islands (Marshall & Baker, 1999). The island populations on Madeira and in the Canary Islands are non-migratory, whilst on the Azores, chaffinches move between islands, but not outside in general these islands are characterised by low seasonality and lower temperature variability (Fernández-Palacios et al., 2011; Kunkel, 2012) .

The islands chaffinches differ from continental birds in a number of ways. Both island chaffinch species are characterised by larger body size, shorter wings, longer beaks and tarsi (Grant, 1979). Male mantle colour is also a distinguishable indigo blue or grey compared to auburn continental birds, but the females are generally similar between continental and island populations (Collar et al., 2010; García-Del-Rey & Gosler, 2005). The song of males also differs quite substantially, in terms of how precisely song-types are learnt (Lynch & Baker, 1993), how predictably phrases are placed into a population-wide syntax (Lachlan et al., 2013), and the speed in which they develop song (see Chapter 3). No prior evidence exists for females from any Atlantic Islands *F.coelebs* subspecies, or *F.teydea* producing song (del Hoyo et al., 2011; Garamszegi et al., 2007).

In this chapter, I report evidence showing that female singing is common in populations of the Atlantic Islands *Fringilla*. Songs produced in multiple populations of *F.coelebs* as well as *F.teydea* will be subject to two main investigations. Firstly, I will conduct bioacoustics comparisons between individuals, sexes and populations within each species to provide descriptions of female song, infer rates of precision of song learning, and assess the level of inter-sex learning. In *F.teydea* I will also include an assessment of rhythmic timing between male and female chaffinches, to see if they fit within established definitions of duetting (Hall, 2009; Hall et

al., 2015; Mennill & Vehrencamp, 2008). Secondly, in order to better determine the function of the song, a series of one and two speaker playback experiments will be run. In addition to this, long-term monitoring of territorial pairs will be used to determine if territories are held throughout the winter in the Tenerife *F.c.canariensis*, unlike *F.c.gengleri* which generally only hold territories between February and July (Marler, 1956a).

4.2 Methods

4.2.1 Field sites, identification and recording protocol

Between 2016 and 2018, evidence of female song was collected from *F.c.gengleri* and *F.teydea* on Tenerife (22/02/2016 - 05/05/2016, 10/05/2017 - 15/05/2017, 17/02/2018 - 30/04/2018), in *F.c.moreletti* on São Miguel, Azores (01/05/2018 - 10/05/2018) and in *F.c.maderiensis* (11/05/2018 - 17/05/2018), as well as further anecdotal recording collections of *F.c.palmae* on La Palma and *F.c.bakeri* (Illera et al., 2018) on Gran Canaria. during April 2017. Control continental populations were also examined in East Sussex, United Kingdom and Catalunya, Spain. 110 male song repertoires were recorded in Catalunya, Spain, along with 105 UK males.

Males from these populations naturally sing in the mornings, with peak song production occurring between 20 mins before sunrise and 12am, and therefore attempted recording of females also took place between these times. Observers detected chaffinches either through audible or visual cues, and females were easily identified from males as both species are highly sexually dimorphic, with males possessing brighter plumage of varied colours. Females are much more similar between populations, all primarily being a duller brown with creamy underparts with an olive-green rump present on all bar *F.c.palmae* (Garcia-del Rey, 2018). Recordings of female song were made opportunistically using a Telinga Pro-8 Twin Science Microphone held in a Telinga parabola of 570mm diameter and digitized at a sample rate of 44.1 kHZ using a TASCAM -DR100.

Unlike male song, female song in both chaffinch species occurs unpredictably; individual females observed regularly over a period of weeks may only vocalise on a single day, if at all. Occasions within which females produced solo song bouts were noted, and comparable numbers of songs recorded for paired males of females were made. To try and entice females to sing, male and female chaffinch song were played intermittently from wireless speakers (UE Boom 2, Logitech). Whilst this rarely provoked previously quiet females into singing, it would often

entice previously recorded females to produce additional songs or to counter-sing alongside their mate. Where possible, song recordings were collected from both the female and their paired male and the GPS co-ordinates of territories for all birds recorded were marked (iPhone 6s, Apple).

4.2.2 Song Analysis

Recordings were processed through the analysis tool Luscinia [Version 2.17.11.22.01, rflachlan.github.io/Luscinia]. Songs were segmented out of larger recordings and presented as spectrograms (base parameters: frame rate 5ms, time step 1ms, max freq. 10,800kHz, high pass filter 1024Hz, dynamic range 40, de-reverberation 100%). For each female, males which had paired with a singing female (paired male hereafter), and a number of unpaired adult males such that both sexes were represented by equal numbers of individuals, two clean song exemplars were selected. Unpaired males were randomly selected from a database of males from each population. Exemplar songs were those which were representative of songs in the birds repertoire and containing little background noise which could affect song measurements. Syllables from each song, identified as individual units of singular or multiple traces of sound interspersed by silent intervals of greater than 10ms, were manually segmented away from background noise. Successive syllables which appeared visually similar on a spectogram were grouped as a repeated syllable phrases. Flourish syllables, buzzy notes which typically occur at the end of male chaffinch song were then also labelled.

4.2.2.1 *F.c.canariensis*

Song comparisons were performed using two methods; basic acoustic comparison, and comparison through a the Dynamic Time Warping Algorithm (DTW hereafter) in Luscinia. To compare differences between male and female song, one exemplar from each recorded female, paired male and unpaired male were selected. The number of songs produced by an individual, number of syllables per song, mean syllable fundamental frequency & mean syllable vibrato amplitude were measured per sex (reported as mean ± SD), and compared between the sexes using Wilcoxon Signed-Rank tests.

To further examine whether *F.c.canariensis* female songs were different to male songs, up to 2 exemplars per individual, from an equal number of males and females, were placed into a DTW in Luscinia. This would include as many mated pairs as captured during recordings. The comparison procedure and weightings was kept identical to those outlined in Chapters 2 & 3 (Table 4.1). To assess whether

female songs are different from males, pairs of songs which scored below 0.075 were classed as belonging to the same type, in line with dissimilarity thresholds used in the previous chapters. K-medoid clustering was performed to produce a global silhouette index for values of k. It would be expected that k=2 would produce optimal clustering, if songs from each sex were significantly different to each other.

Table 4.1: Acoustic metrics and settings used in the DTW

Acoustic Metric	Weighting	Time Warp Setting	Value
Time	1	Compression Factor	0.2
Fundamental frequency	0.9	Maximum Warp	100%
Fundamental frequency change	0.86	Stitch threshold (ms)	30
Vibrato Amplitude	0.05	Cost of alignment error	0.2
Fundamental frequency norm	1.26		

To examine the level individuality in female song, individuals with greater than 5 songs analysed, had their songs placed through a seperate DTW. These were then clustered using Wards Method. To examine repertoire size, individuals which had greater than 30 songs analysed, had their songs placed through another DTW. These are then presented visually through non-metric multidimensional scaling (NMDS) plots, using methods outlined in Chapter 2, with the number of song-type clusters assessed visually.

4.2.2.2 *F.teydea*

In *F.teydea*, basic acoustic comparisons as well as comparison through DTW were again performed. For the basic acoustic comparison, female song, male song, male song flourish syllables and contact calls produced by both sexes were compared for mean syllable fundamental frequency & mean syllable vibrato amplitude using Wilcoxon Signed-Rank tests. To further assess whether male and female songs differed, up to 2 exemplars per individual, from an equal number of males and females, were placed into a DTW in Luscinia, and again all possible mated pairs were included. Pairs of songs which scored below 0.075 were classed as belonging to the same type. K-medoid clustering was performed to produce a global silhouette index for values of k. It would be expected that k=2 would produce optimal clustering, if songs from each sex were significantly different to each other.

Additional analysis was also performed females, to assess whether song was produced in a non-random timing relative to their partnered male. Pairs of naturally singing *F.teydea* were recorded for at least 2 consecutive minutes. The

percentage of female song which either overlapped or had its onset within 1 second of the end of a male song were measured. This was then compared to the proportion of female singing overlap that would be expected to occur given the number of songs produced by a female during the recording spell, and the time males spent singing + 1 second per song. This would be compared for each pair through a Wilcoxon signed rank test. This is in line with previous assessments of evidence of duetting from other species (Hall et al., 2015).

4.2.3 Female song function

To test territorial responses to female song, a series of playback experiments were conducted on the Tenerife subspecies of *F.coelebs*, *F.c.canariensis* and *F.teydea*.

4.2.4 Playback experiments - *F.c.canariensis*

Two, two-speaker playback experiments were performed on *F.c.canariensis*. To test whether female song instigated a response from conspecifics, example songs were presented alongside an unheard control. The selected control were songs of a swamp sparrow *M.georgiana*, a species alien to chaffinches, for which a database of previously recorded individuals was readily available (Lachlan et al., 2018). To test the strength of female song in territorial interactions, in a second playback experiment female song was presented alongside male song.

Playback studies were carried out at the Parque Natural Corona Forestal (28.42, -16.38) and Parque Rural de Anaga (28.52, -16.25), between 23rd April and the 7th May 2015. Each stimuli consisted of two sets of songs either side of a stereo recording, with one channel assigned to a stimulus set. Songs were paired together based upon similarity in song length. Each set consisted of 12 repetitions of an exemplar song, and each set utilised a different song exemplar recording, to minimise pseudoreplication (McGregor, 2000). Stimuli were processed using the Audacity software package. Songs were normalised for amplitude (3db) and modified for playback track production (band pass filtered for 1000-10000Hz, 0.3s fade in, 0.3s fade out). In addition, *M.georgiana* control stimuli underwent a pitch change reduction by 3KHz, to an average of around 6KHz, to be similar in frequency range to the songs of *F.coelebs*. Each song was broadcast every 10 seconds to reflect counter-singing rates in both *F.coelebs*. One set beginning 5 seconds in front of the other, to prevent stimuli from overlapping. The first stimuli set broadcast, as well as the speaker designated to a stimuli type were counterbalanced to prevent biases in approach to the first heard stimuli or to one speaker.

We identified previously untested chaffinch pairs that were occupying established territories and assessed territory boundary interactions during prior dawn visits to ascertain the centre of each territory. Trials took place between 0700hrs and 1100hrs on a subsequent clear day. Two Bluetooth speakers (UE BOOM 2, Logitech) were placed 16m apart at the centre of a territory, with distance markers placed at 1,2,4 and 8m intervals either side of the speaker to improve estimation of approach distances. Speaker amplitude were set at the same level and were placed within equal distance of a suitable close approach perching point (<50cm).

Once setup, contact calls were intermittently produced from both speakers until the pair were both detected, and once this occurred, a period of 1 minute ambient noise was instigated. After this, the 2-minute active playback period began, which was followed by an additional 5 minutes of ambient noise. Across the total of 7 minutes, an observer would dictate the approximate locations of each bird in relation to the speakers in 5 distance bins (<1m, 2m, 4m, 8m, >8m) into a voice recorder (iPhone 6s, Apple). In the event that one speaker was not approached by either sex throughout the trial, the approached stimuli was then broadcast out of the non-approached speaker after the trial, to determine if speaker placement influenced this lack of approach instead of the stimuli. If individuals failed to approach this speaker, then the results of this playback were not included.

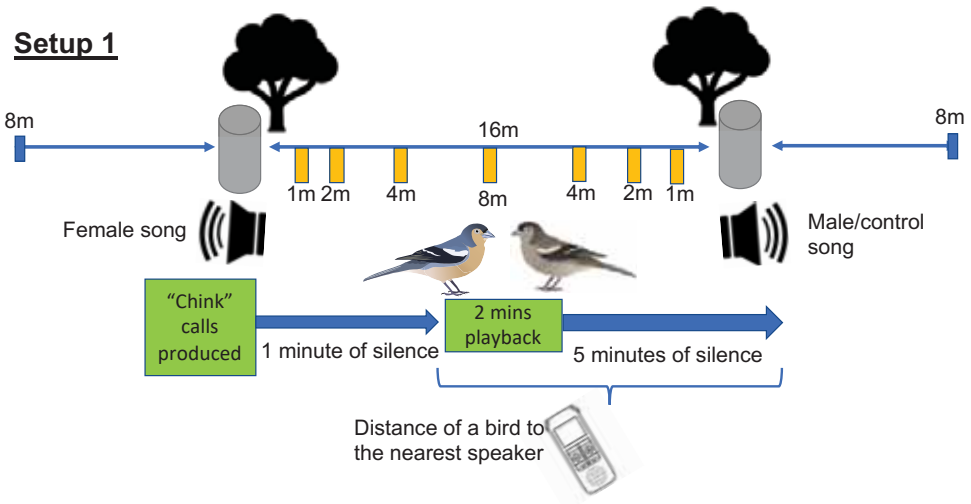


Figure 4.1: Pictoral representation of the playback setup and protocol for the female vs control, and female vs male playback studies. 2 speakers (grey cylinders) are placed 16m apart, with markers (yellow) indicating distance to an observer. An observer measures the approach of both the male and female of a territorial pair towards either a speaker broadcasting female song or another type of song depending upon the experiment

4.2.5 Playback experiments - *F.teydea*

A further two playback experiments were conducted on *F.teydea*. To assess whether female song would instigate a different response to a conspecific song, female song was presented alongside the same *M.georgiana* stimuli used with *F.c.canariensis*. Playbacks stimuli creation, presentation order, trial timings, response distance measurements and response measures were all replicated from the *F.c.canariensis* study.

To test whether duetting served increased territorial function compared to solo singing, we conducted a repeated-measures one-speaker playback design. We used three stimuli set types; male solo song, female solo song and duet. To create stimuli, recordings of both individuals from a pair were collected, with playback stimuli modified as described above. These were then tested on birds holding a distant territory to where the stimul were created (>5km) to remove a potential impact of song familiarity. Each duet stimuli set was formed of a previously untested song type per sex, with one broadcast solely on the left channel, and the other on the right. These were counterbalanced across all trails. Male song stimuli were presented 12 times every 10 seconds, with female songs placed randomly $\pm$ 1 second a male song ending to reflect how the duet is performed in naturally singing birds. To create solo song stimuli sets, one speaker channel was muted. The three stimuli sets were presented to 9 territorial pairs, with a minimum of 1 and maximum of 3 day interval between each trial. Trial order was manually balanced to minimise the impact of order on response.

Territories of *F.teydea* pairs were identified as per two-speaker trials above. Two speakers were placed in the territory for all trials, with just one speaker broadcasting during solo singing trials. Both speakers were placed within 50cm of each other, between 1-2.5m from the ground, and within 50cm of the nearest perching point. Speaker positions and reference markers were kept identical between trials for each pair. Playback broadcast and notation methods were the same as for the two-speaker trials above.

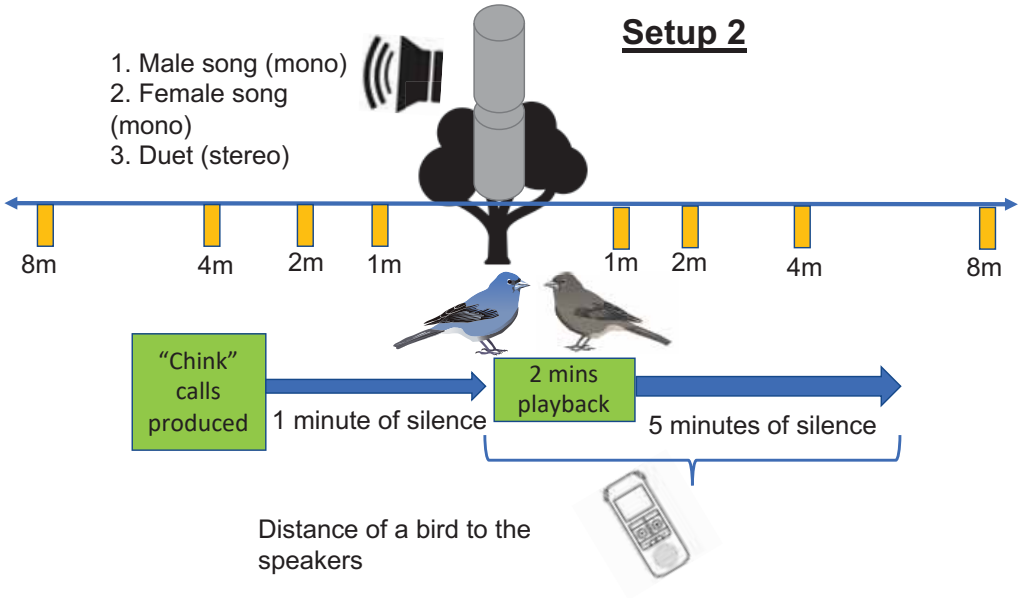


Figure 4.2: Pictoral representation of the playback setup and protocol for the duetting playback study. 2 speakers (grey cylinder) are placed within the same tree, with 1 speaker broadcasting playback in the mono playback, or both in the stereo playback.

4.2.6 Playback response measures and statistical analysis

Assessment of playback responses in two-speaker trials was measured using 4 parameters based upon Leitão and Riebel (2003); a similar playback experiments conducted on chaffinches. These were:

1. time to approach a speaker
2. closest approach to the speaker
3. time spent within 2m of the speaker
4. time spent between 2-4m of the speaker

Scoring began at the beginning of the first playback and was assessed over the subsequent 6 minute total observation period. The locations of both the male and female for the pair were noted for every 5 seconds of the observation period. If a bird did not approach a speaker the latency to approach was set at the maximum time interval of 6 minutes. To compare the response of territorial pairs to speakers using the approach metrics, mean responses were compared between each sex using two-tailed Wilcoxon signed-rank tests. All statistical analyses were carried out in R (Team, 2015).

In addition, we calculated a proportional response score based upon time spent

within proximity to each speaker. Distances from each speaker were weighted such that halving the distance scored double. Scores were then converted into a proportional response to either speaker (Score speaker L/R / Score speaker L + Score speaker R) and calculated for the 2 minute active playback period. Each pair, and then individuals in each sex was then compared using two-tailed Wilcoxon signed-rank tests (treating sample size as each pair tested as interactions between pairs may have influenced each other).

In the duetting playback study performed exclusively on *F.teydea*, to analyse if territorial pairs responded more to duetting in the repeated measures playback we conducted a PCA in R on a correlation matrix for the 4 response metrics. We then fit a multivariate linear mixed model using the MCMCglmm package (Hadfield, 2010). The first principle component of the response metrics (loadings and proportion of variance stated in the results) was the response variable, with sex, stimuli type and order as predictors and territorial pair as a random effect. We utilised the default prior (see Hadfield (2010) for details). The MCMCglmm chain contained 100,000 iterations with a burn-in period of 10,000 and a thinning interval of 10, resulting in 9000 samples. Tests were performed both for responses over the 2 minute active playback period as well as the 7 minute overall trial.

4.2.7 Territorial behaviour in *F.c.canariensis*

To test whether territory defence was maintained throughout the year, 12 territorial adult males were captured in mist nets and colour ringed by local field biologist Eduardo Garcia del-Rey during the 2015 & 2016 breeding season. Territories were re-visited by Eduardo on the 15th and 29th December 2016, a point at which we would not typically expect males to occupy their breeding season territory or respond to conspecific playback (Marler, 1956a). Thus if this continued to be the case for *F.c.canariensis* it would be expected that no colour ringed individuals would be recovered in winter territory visits.

4.3 Results

4.3.1 Recording effort

4.3.1.1 *F.coelebs*

130 field days produced at least 433 hours of total active search time of female song in island *F.coelebs* subspecies. Of this, 370 hours were made on Tenerife, 42 hours on São Miguel, and 21 hours on Madeira. In addition to this, anecdotal recording collection was made in both La Palma and Gran Canaria alongside

data collection of male singing (Lachlan, unpublished). 4 subspecies of *F. coelebs* were detected producing female songs, with a total of 21 individuals recorded in sufficient quality for further analysis. 18 female *F.c.canariensis* were recorded on Tenerife, and sole recordings were made of *F.c.bakeri* in Gran Canaria, *F.c.palmae* in La Palma and *F.c.moreletti* on the Azores (Table 4.2). No individuals were recorded in the Madeira visit or in either continental Europe population.

Female song was first detected on the 23rd February 2016, the second day of surveying on Tenerife. Whilst this individual continued to sing, sightings of other singing females were not made until the until 29th March. A further 19 individual females were subsequently heard and noted as producing female song but were not captured in recordings. At least 14 recorded females were paired with a male upon recording. However, both of the females which were recorded on >3 occasions were individuals which were not observed to be paired with a male. One female was captured through mist netting and was aged as being in at least its second breeding season. The male paired with this individual was a yearling in its first breeding season (JTench07 from Chapter 3).

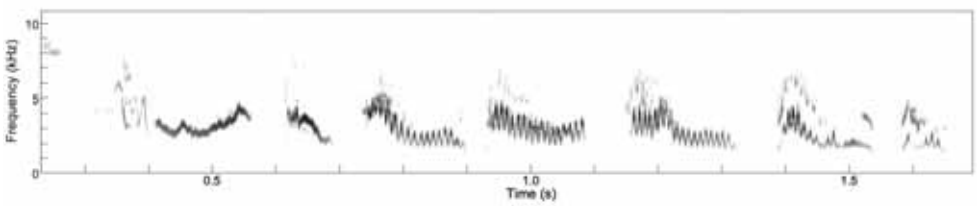
Across our populations, females were found to sing much less than males. In Tenerife, sampling of both males and female song occurred between 18/04/2016 and 25/04/2016 over a total of 31 hours. During this time, 37 males were recorded with a mean of 74.35 ± 25.23 song recordings per individual, whilst 8 females were recorded for a mean of 29.23 ± 17.54 song recordings per individual. This time period represented the highest recording rates of female song for any sampling week in the study, accounting for 38.10% of all individuals captured (Table 4.2). Other spells of recording yielded far fewer females. On São Miguel, 42 hours of fieldwork yielded 65 males recorded with a mean of 43.21 ± 16.14 songs per individual, but just 1 female for which 6 songs were captured. Across the total time period for which male and female song recording was comparable (15 recording days with 82 hours of surveying), significantly fewer females were recorded per day than males (Mdn males per day = 6, Mdn females per day = 0, Wilcoxon rank-sum test, W=0, $p<0.005$), and those females that were recorded produced significantly fewer songs (Mdn songs recorded per session in 112 males = 33, Mdn songs recorded per session in females = 15, Wilcoxon rank-sum test, W=162, $p<0.011$).

Females rarely sang in solo bouts, and generally song was produced alongside those of surrounding males. Recording sessions made during the dawn chorus (between 20 mins before sunrise and 20 mins after sunrise) accounted for 35% of recording sessions of female song (Figure 4.4), whilst 24% of recording sessions

Table 4.2: Locations and song recording figures for *F.coelebs* females

Territory Latitude	Territory Longitude	Recordist	Subspecies	Name	First Recording	Last Recording	Songs Recorded	Recording Days
28.333	-16.817	JC	*F.c.canariensis*	FTench01	08/05/2017	08/05/2017	5	1
28.537	-16.299	JC	*F.c.canariensis*	FTench02	22/04/2016	22/04/2016	39	1
28.531	-16.281	JC	*F.c.canariensis*	FTench03	23/02/2016	13/04/2016	304	7
28.336	-16.759	JC	*F.c.canariensis*	FTench04	25/02/2018	06/03/2018	16	2
28.330	-16.810	JC	*F.c.canariensis*	FTench05	20/02/2018	20/02/2018	2	1
28.354	-16.497	JC	*F.c.canariensis*	FTench06	22/04/2016	22/04/2016	6	1
28.448	-16.386	JC	*F.c.canariensis*	FTench07	21/04/2016	21/04/2016	12	1
22.446	-16.385	JC	*F.c.canariensis*	FTench08	15/04/2016	21/04/2016	57	2
28.540	-16.298	JC	*F.c.canariensis*	FTench09	15/04/2016	15/04/2016	24	1
28.528	-16.310	JC	*F.c.canariensis*	FTench10	17/04/2016	17/04/2016	5	1
28.442	-16.378	JC	*F.c.canariensis*	FTench11	03/04/2016	03/04/2016	4	1
28.332	-16.816	JC	*F.c.canariensis*	FTench12	25/04/2016	25/04/2016	21	1
28.329	-16.808	JC	*F.c.canariensis*	FTench13	10/05/2017	10/05/2017	18	1
28.328	-16.809	JC	*F.c.canariensis*	FTench14	25/04/2016	25/04/2016	16	1
28.358	-16.510	JC	*F.c.canariensis*	FTench15	22/04/2016	22/04/2016	63	1
28.332	-16.811	JC	*F.c.canariensis*	FTench16	22/04/2016	22/04/2016	42	1
28.448	-16.386	JC	*F.c.canariensis*	FTench17	27/04/2016	27/04/2016	4	1
28.357	-16.508	JC	*F.c.canariensis*	FTench18	20/04/2016	20/04/2016	51	1
37.878	-25.746	JC	*F.c.mortelli*	FAzores01	03/05/2018	03/05/2018	5	1
NA	NA	RFL	*F.c.palmae*	FPalmae01	16/05/2017	16/05/2017	3	1
NA	NA	RFL	*F.c.bakeri*	FGranC01	27/04/2017	27/04/2017	2	1

(a)



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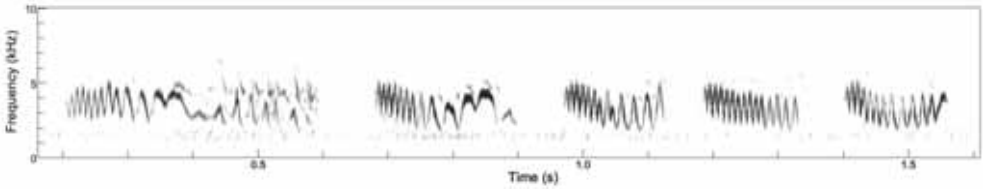

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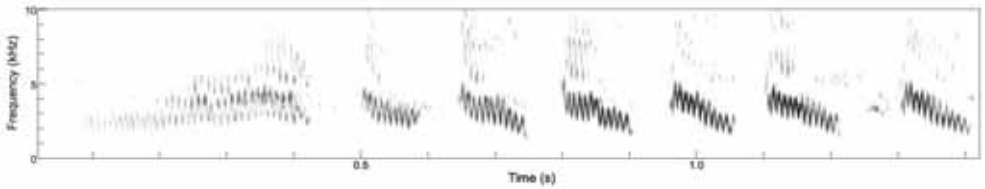

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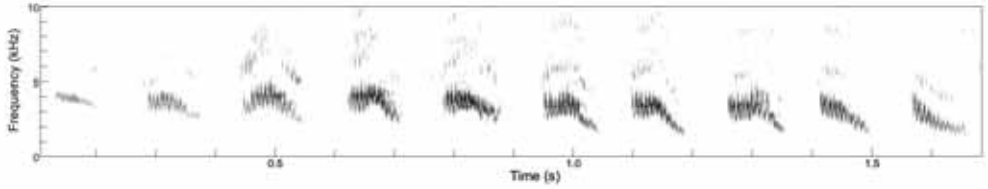

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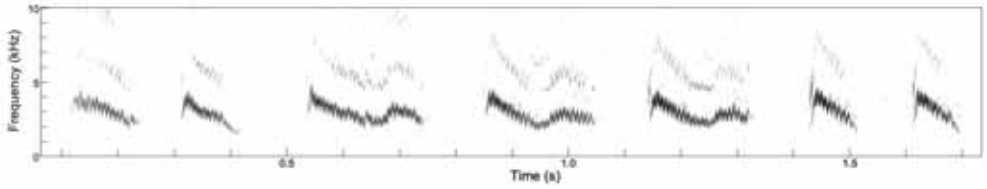


Figure 4.3: 5 spectrograms of exemplar songs recorded from female *F.c.canariensis* in Tenerife.

coincided with the singing of a partner male. One female proved to be a regular exception to this, with over 250 songs recorded on 11 different occasions between 23rd February and 13th April 2016, often without instigation from surrounding males or playback.

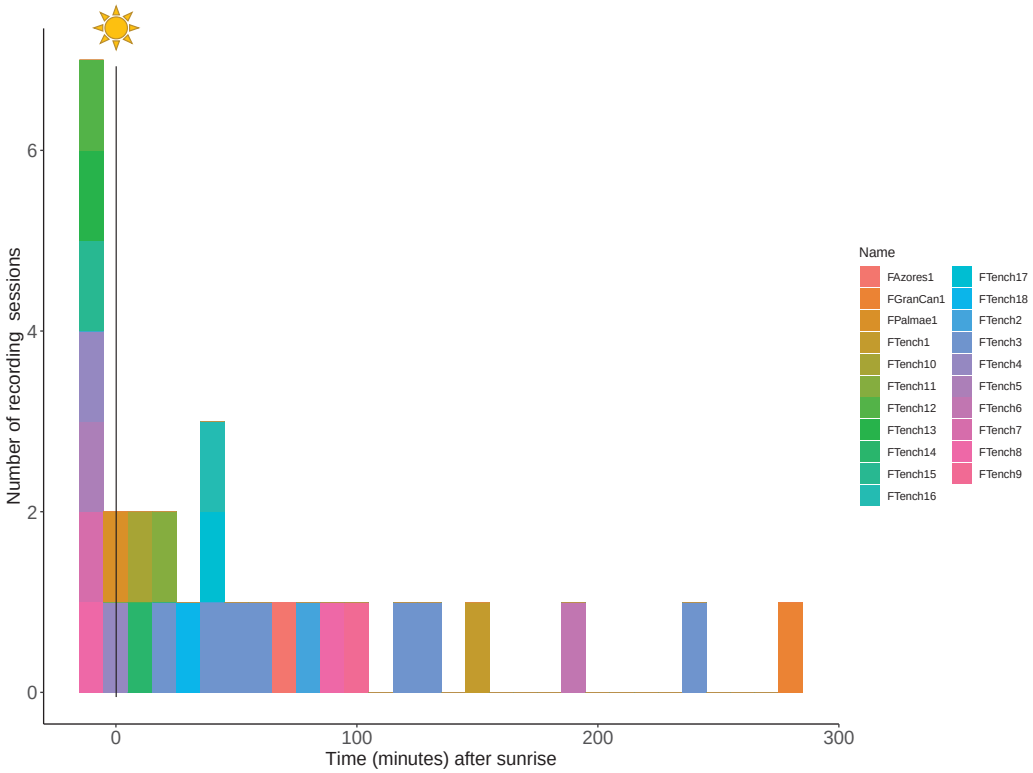


Figure 4.4: The distribution of the start of recording sessions for female songs, in relation to sunrise. Each individual is coloured separately, as marked by their individual identifier code.

Female songs were audibly distinguishable from males in the field. Predominantly, they were identified through being short songs formed of a series of harsh buzzy syllables (Figure 4.3). 21 exemplar songs per sex (1 per individual) were compared for differences in syllable fundamental frequency, vibrato amplitude and syllable number (Figure 4.5). Female songs were formed of significantly less syllables than males (females 7.05 ± 2.99 syllables, males 32.58 syllables ± 7.45, Wilcoxon rank-sum test: W=342, p <0.0001). Female syllables had significantly higher mean vibrato amplitude than male song syllables in general (Mdn female 444.3Hz, Mdn male 0Hz, M male 83.59Hz, Wilcoxon rank-sum test: W= 16121, p <0.001) though not when exclusively compared to male flourish syllables (Mdn male flourish 735Hz n= 23, compared to 149 female syllables; Wilcoxon rank-sum test: W= 1573, p = 0.35). The mean fundamental frequency of female syllables was not found to significantly differ to that of males (Mdn female 3.07kHZ, Mdn male 3.02kHz, Wilcoxon rank-sum test, W = 55957, p = 0.13). When songs were clustered using Ward's Method, male and female songs clustered separately in all

individuals, save for one female (Figure 4.6). The highest global silhouette index value for clustering solutions produced by a k-medoids clustering algorithm was 2 (Figure 4.7), indicating these songs are best grouped into 2 categories. The four mated pairs included in the clustering solution were not found to cluster together, and male-female pairs were no more similar to each others songs, than would be expected of another member of the opposite sex (Figure 4.6).

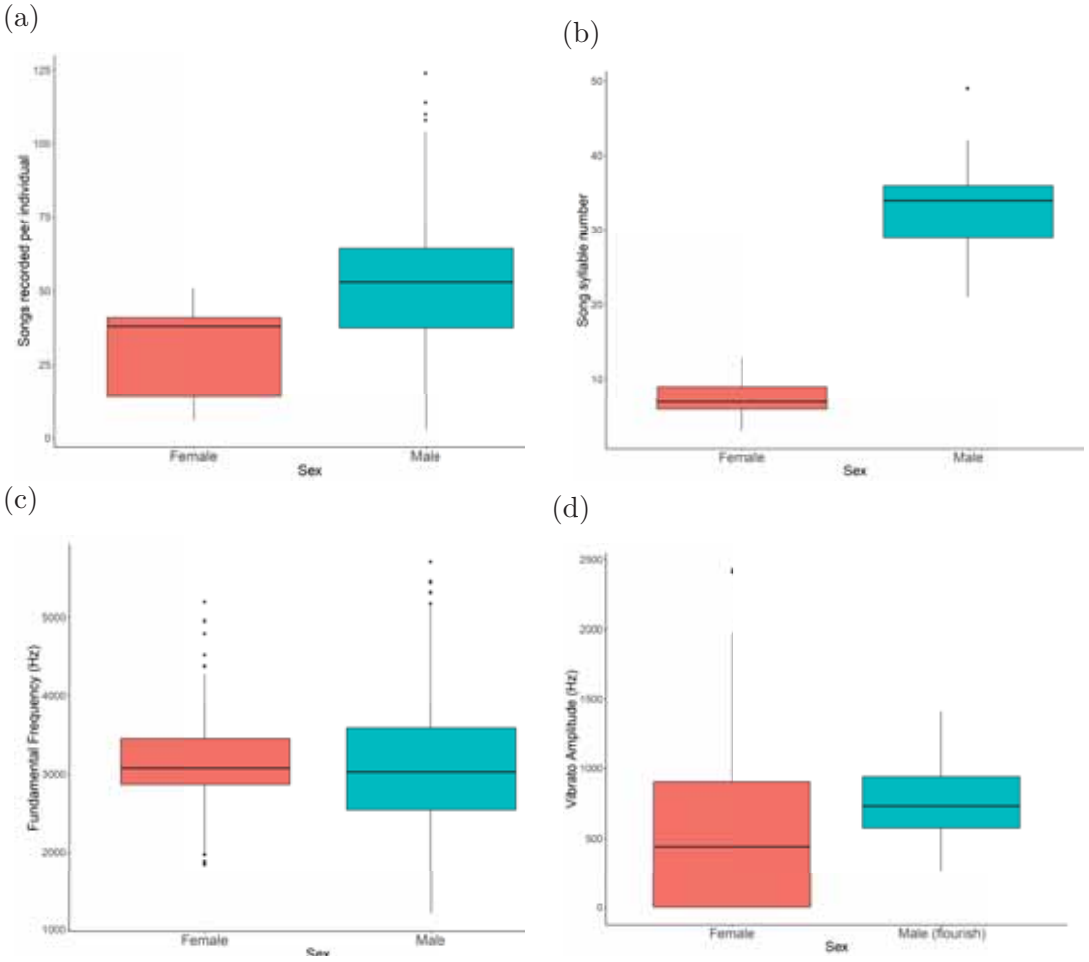


Figure 4.5: Distribution of four song characteristics male and female *F.coelebs* songs, a) the number of songs collected per individual, b) the number of syllables each song contained, c) the fundamental frequency of song syllables, d) the vibrato amplitude of the female songs and male flourish syllables.

For examining individuality, 6 individuals met the criteria of having 5 songs analysed as exemplar recordings. Within these songs, individuals clustered separately to each other, save for 1 song produced by Ftench15, which was isolated from its other songs (Figure 4.8). Even when 30 or more song recordings per individual were compared (n=3 individuals), songs still clustered within individuals (Figure 4.9). In terms of repertoire size, no female produced songs which would be clearly placed into any more than one song-type category. In the 3 females where 30 or more song recordings were analysed, each individual was represented by one

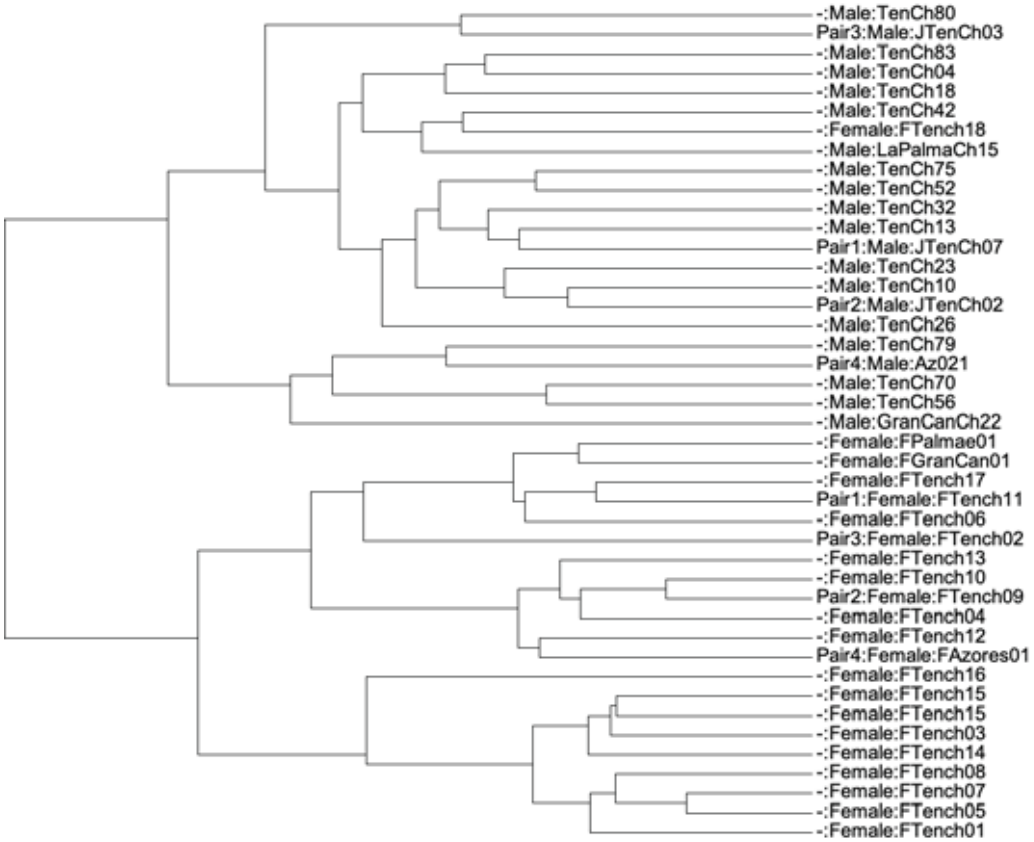


Figure 4.6: Dendrogram of exemplar songs taken from male and female *F.c.canariensis*, with male exemplars taken from recordings made by RF Lachlan. Branch depth between pairs equates to song dissimilarity as calculated through the DTW, which is then clustered using Ward's Method. Branches are labelled by whether the individuals are paired with a female included in the comparison, with pair numbers identifying mated pairs, an individuals' sex and their identifier code.

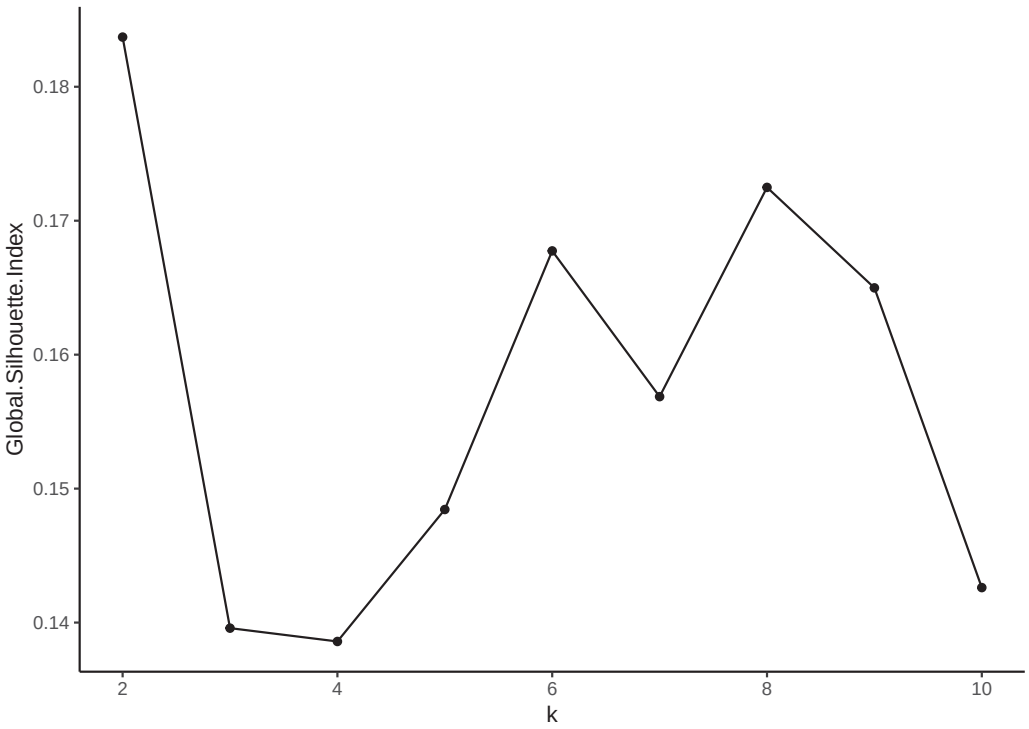


Figure 4.7: Global silhouette index for different values of k, as produced when a k-medoids clustering algorithm is applied to exemplar songs from male and female *F.c.canariensis*. A greater index value is indicative of greater clustering tendency. The peak was k=2, indicating that the data naturally best clusters into 2 groups (male and female).

cluster, indicating that all songs produced by the individual were more similar to each other, than to the songs of other individuals (Figure 4.8).

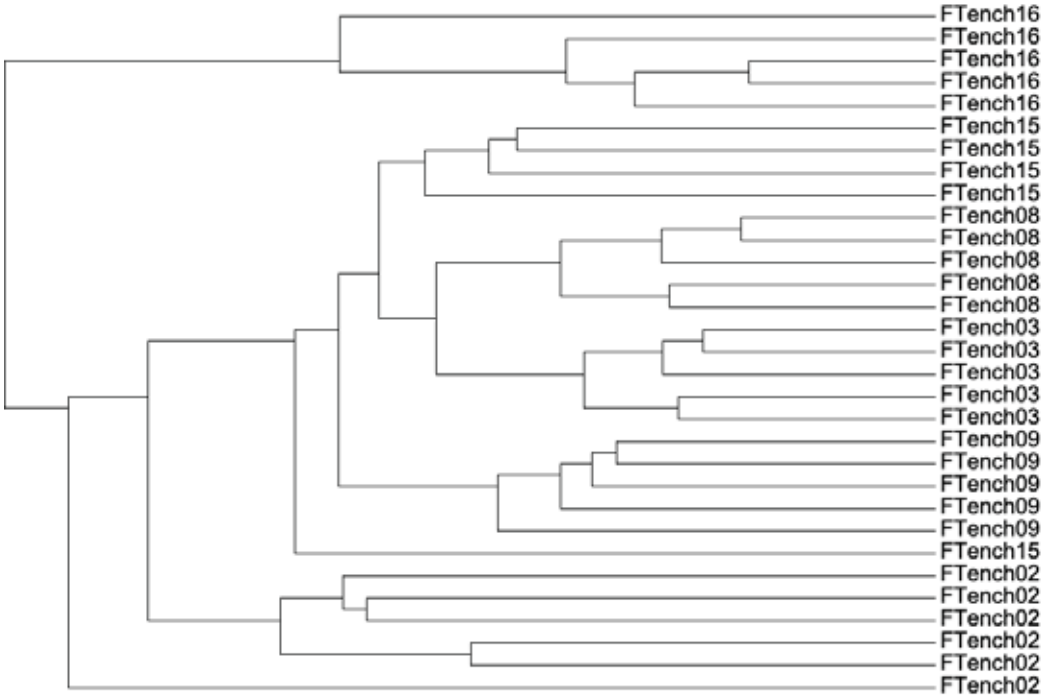


Figure 4.8: Dendrogram of 5+ exemplar songs in 6 female *F.c.canariensis* individuals. Branch depth between pairs equates to song dissimilarity as calculated through the DTW, which is then clustered using Ward's Method. Branches are labelled by an individual's identifier code.

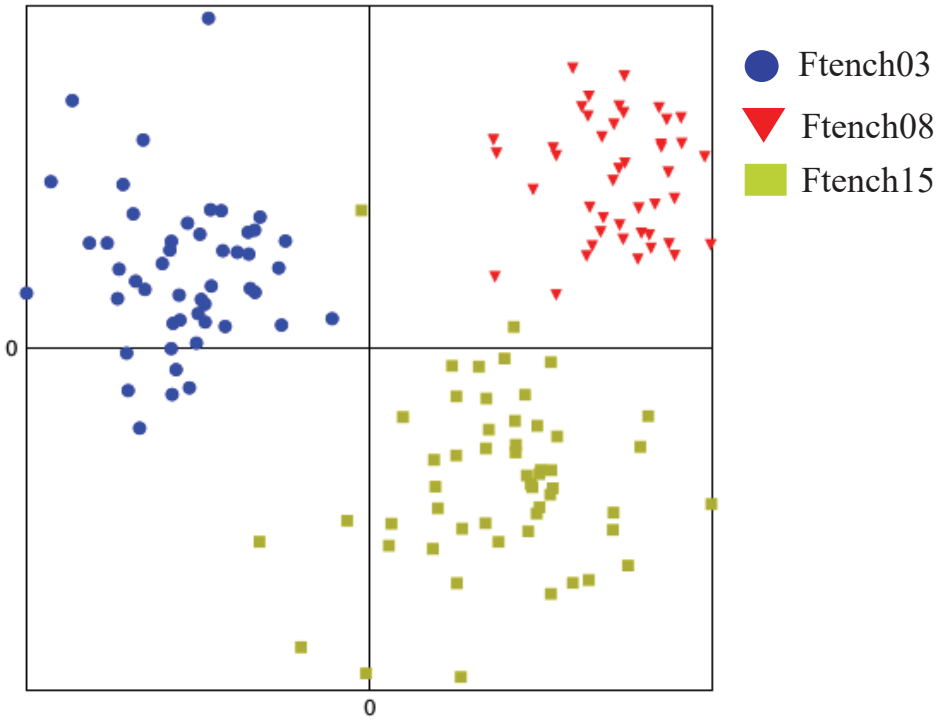


Figure 4.9: NMDS plot of song dissimilarity taken from*F.c.canariensis* females. Each point represents a song. The distance between any two points reflects their acoustic similarity as measured through the DTW. Each of the 3 individuals included is represented by a different colour.

4.3.1.2 *F.teydea*

58 days of surveying within *F.teydea* breeding habitat resulted in 208 hours of total search time for female song. 30 individual *F.teydea* females were recorded singing in this time (Table 4.3). This equated to 39% of territory visits, compared to males, which were recorded in 81% of visits.

F.teydea females produce different songs to *F.teydea* males. In 149 song recordings, 146 songs consisted of a single buzzy syllable (Figure 4.10). On individual, produced a two-syllable song, on three different recordings. One exemplar from each of 36 individuals were collected from each individual female and compared with 36 male song exemplars, 14 of which were mated pairs. Males had significantly greater syllable counts (female syllable number, 1.03 ± 0.25 male syllable number 19.96 ± 8.99, Wilcoxon rank-sum test, n = 57, W = 812, p >0.0001). Overall, female syllables were buzzier and significantly greater in mean vibrato amplitude compared to male syllables (Mdn female 681.4 Hz, Mdn male 0 Hz, M male 18Hz, Wilcoxon rank-sum test, W = 1951, p <0.0001, Figure 4.11). Similarly to

Table 4.3: Territory location and number of songs recorded in female *F.teydea*

Territory Latitude	Territory Longitude	Name	Recording Date	Songs Recorded
28.169	-16.637	BC02F	11/04/2017	11
28.172	-16.638	BC04F	11/04/2017	1
28.172	-16.637	BC05F	11/04/2017	1
28.171	-16.617	BC11F	13/04/2017	7
28.17	-16.617	BC14F	13/04/2017	4
28.147	-16.674	BC15F	14/04/2017	1
28.171	-16.674	BC18F	16/04/2017	1
28.186	-16.655	BC19F	22/04/2017	3
28.186	-16.654	BC20F	22/04/2017	3
28.37	-16.467	BC21F	04/05/2017	4
28.411	-16.412	BC22F	19/05/2017	2
28.186	-16.673	BC23F	19/04/2017	1
28.418	-16.422	BC24F	14/05/2017	1
28.419	-16.432	BC27F	16/05/2017	2
28.418	-16.423	BC30F	17/05/2017	5
28.419	-16.417	BC33F	17/05/2017	1
28.411	-16.412	BC34F	04/03/2018	7
28.181	-16.642	BC39F	17/05/2017	6
28.419	-16.41	BC40F	12/05/2017	6
28.419	-16.423	BC41F	17/05/2017	1
28.411	-16.43	BC43F	17/05/2017	8
28.416	-16.427	BC44F	17/05/2017	13
28.415	-16.428	BC45F	18/05/2017	12
28.185	-16.584	BC46F	04/03/2018	8
28.182	-16.594	BC49F	04/03/2018	2
28.174	-16.604	BC50F	21/05/2017	15
28.183	-16.591	BC62F	05/03/2018	8
28.183	-16.592	BC63F	05/03/2018	8
28.173	-16.642	BC64F	05/03/2018	4
28.173	-16.641	BC66F	06/03/2018	2
28.188	16.577	BC67F	06/03/2018	1
28.332	-16.74	BC68F	06/03/2018	3
28.252	-16.769	BC69F	10/03/2018	3

F.coelebs no difference was found between the vibrato amplitude of female songs compared to male flourish syllables (Mdn flourish 467.7Hz, n = 119 male flourish syllables, Wilcoxon rank-sum test, W = 2067, p >0.05), however the fundamental frequency was significantly higher in female songs (Wilcoxon rank-sum test, female FF 2982.03 ± 378.90, male FF 2540 ± 378.90, W=688, p <0.001, Figure 4.11).

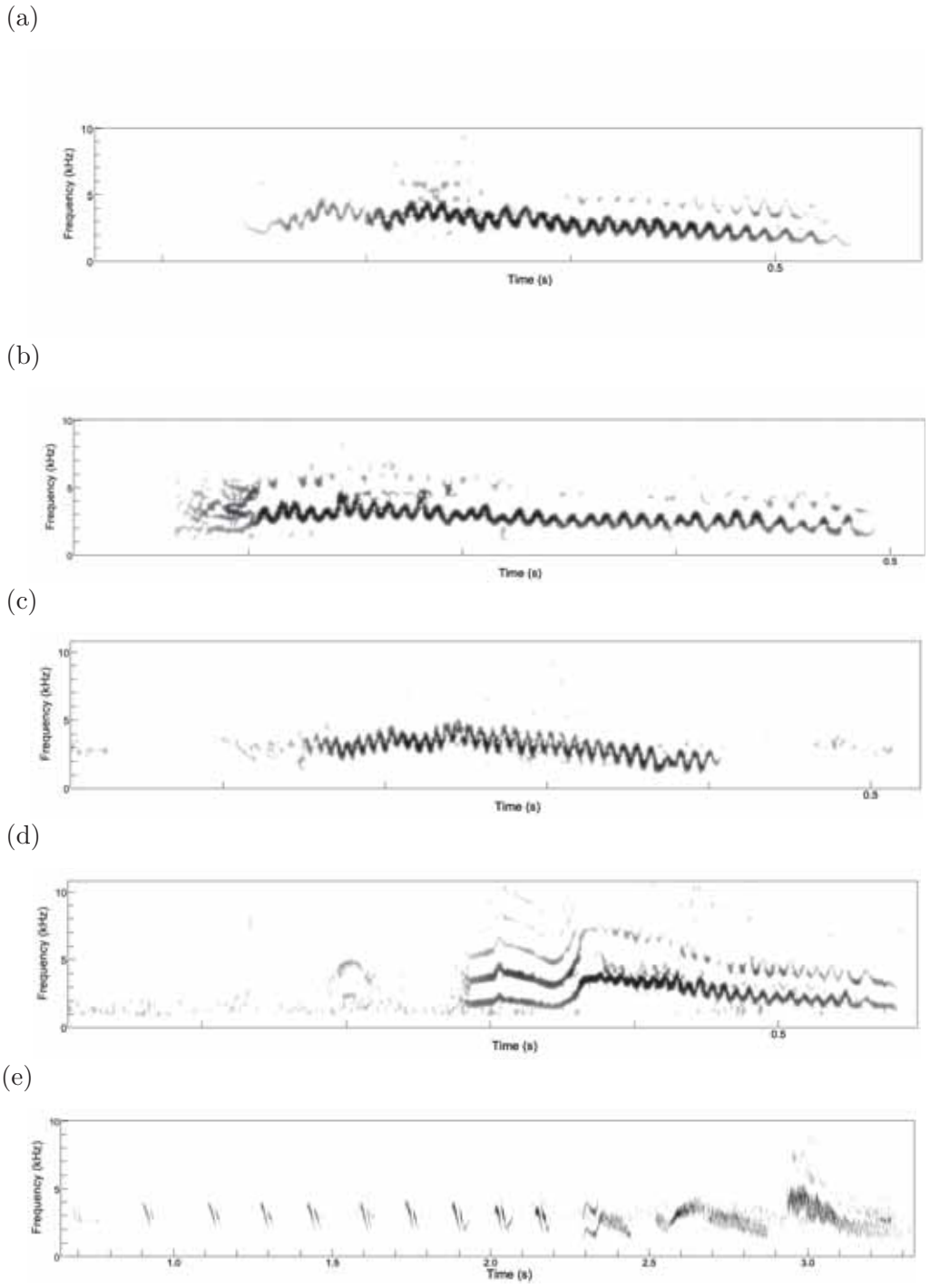
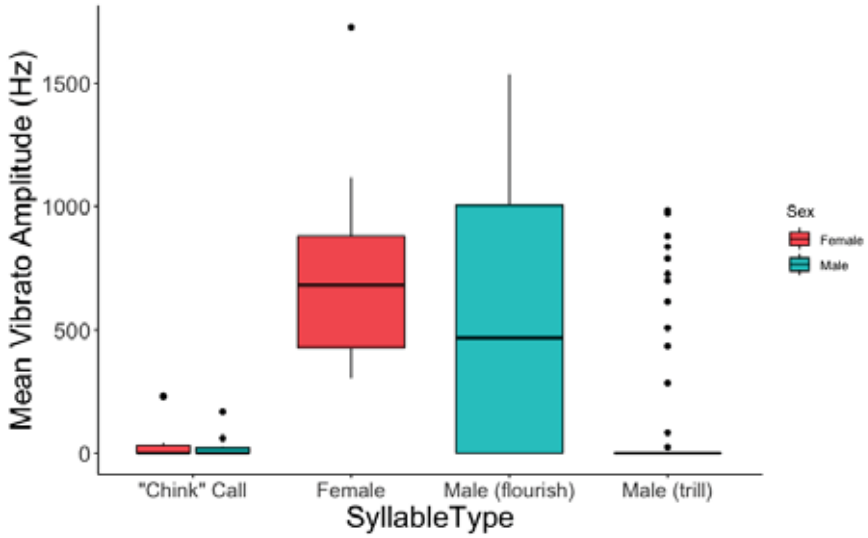


Figure 4.10: Spectograms of 5 songs recorded in *F.teydea*. Spectrogram e) includes a typical example of a female song produced alongside a male song. The female song in this case is the lattermost syllable visible on the spectogram

(a)



(b)

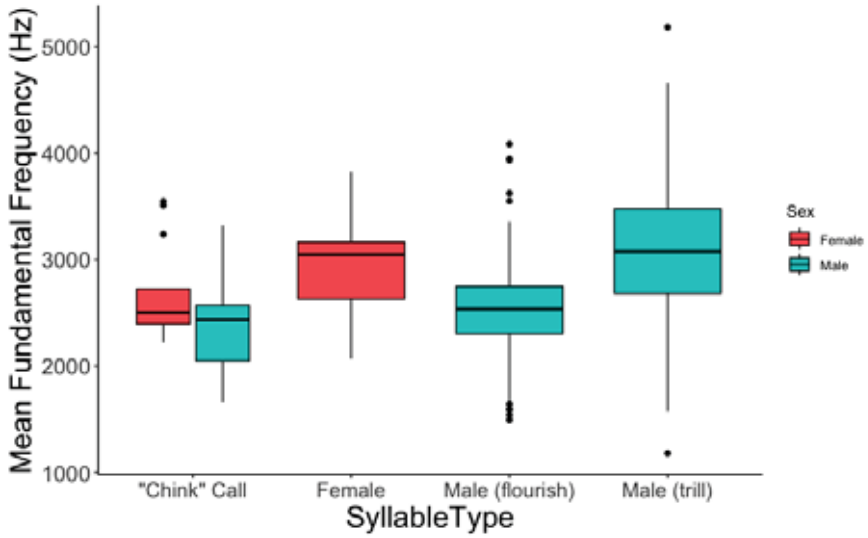


Figure 4.11: Types of *F.teydea* vocalisation in relation to two acoustic characteristics

When the DTW dissimilarity scores for the male and female exemplars were clustered using Ward's Method, the songs of males and females clustered separately (Figure 4.12). There was no evidence to suggest clustering of songs from mated pairs used more frequently by males and females of a pair, than unpaired birds.

No individual was recorded more than 15 times, and therefore determining repertoire variability could not be achieved using the same methods as for *F.coelebs*. To provide an assessment of both repertoire size and individuality, songs from females with greater than 5 songs analysed (n=6), were placed through a DTW. The dissimilarity scores were then clustered using Ward's Method. Of the 42 songs included, 29 were least dissimilar to one produced by the same bird. Across *F.teydea* degree of dissimilarity between individuals was much lower than in female *F.coelebs*. In the 862 song comparisons conducted in the DTW in this latter analysis, 74.6% fell under the 0.075 threshold for belonging to the same song-type category.

Female songs were generally only produced in conjunction with male song (see below), usually in response to a genuine territorial invasion, neighbour song, or to a playback song recording. 14 recordings of the common contact call used by both sexes of blue chaffinches (n= 7 per sex, example Figure 4.14a,4.14b) were ran through a DTW alongside 32 female exemplars to assess acoustic differences. A song NMDS plot revealed that these calls would cluster together regardless of sex,and seperately from female songs (Figure 4.14c). Female song syllables were far buzzier than calls resulting in significantly different vibrato amplitude rates (Vibrato amplitude female syllable Mdn 681Hz, contact call Mdn 0Hz, contact call Mean 31Hz, Wilcoxon rank-sum test, $W = 21.5$, $p > 0.001$). In over 5000 song recordings of 120 male *F.teydea* (Lachlan, unpublished data), no complete song produced resembled a typical female song when viewed on a spectogram, though partial songs of the males which have the initial trill phrase removed, can . However, these are typically lower in freuqency, as stated above. All individuals labelled as females had been observed to possess plumage typical of females, when viewed in the field.

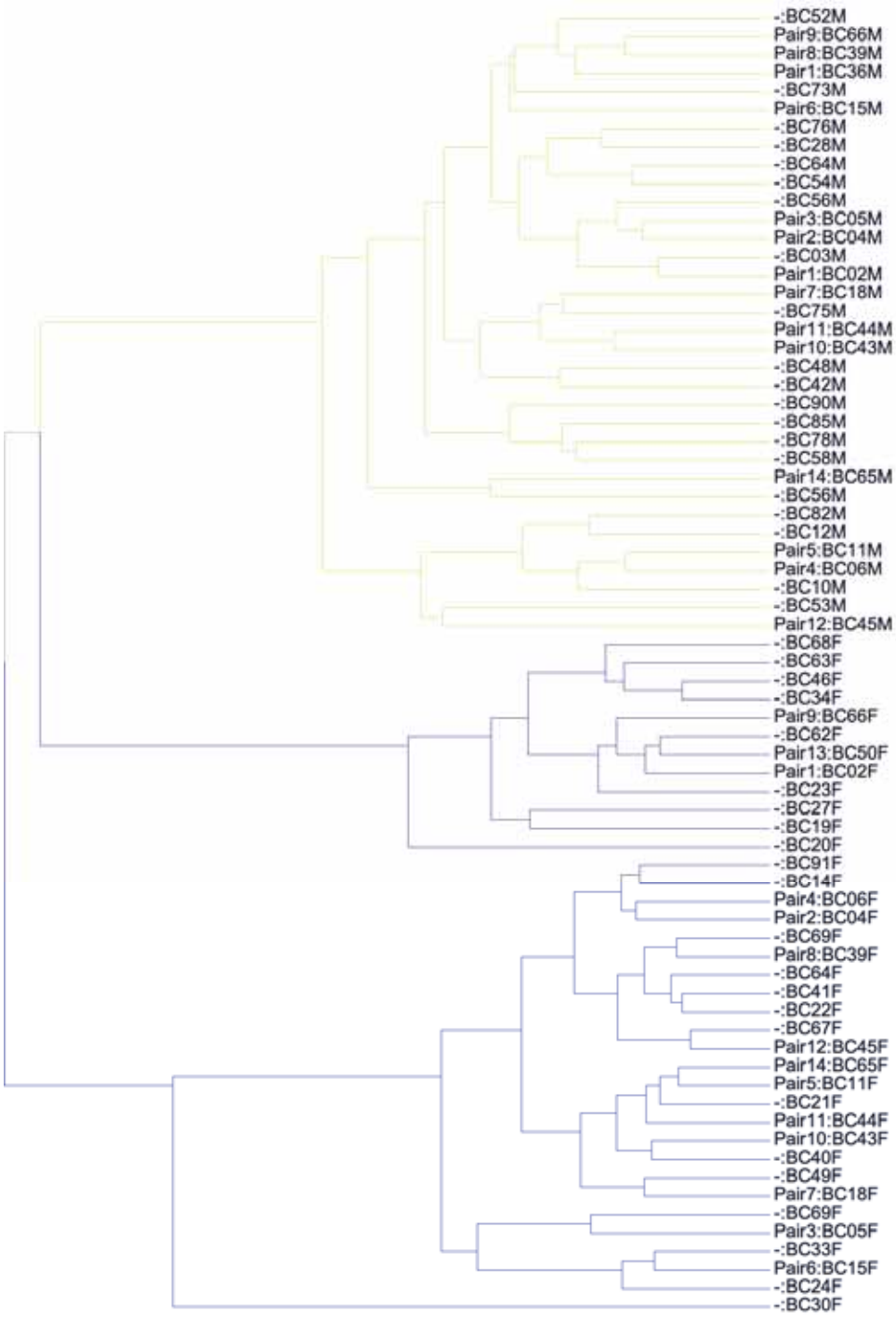


Figure 4.12: Dendrogram of exemplar songs taken from male and female *F.teydea*, including male exemplars taken from recordings made by RF Lachlan. Branch depth between pairs equates to song dissimilarity as calculated through the DTW, which is then clustered using Ward's Method. Branches are labelled by whether the individuals are paired with a female included in the comparison and their individual identifier, which ends in M for males and F for females. In addition, branches of females are coloured in blue, and branches of males are in yellow.

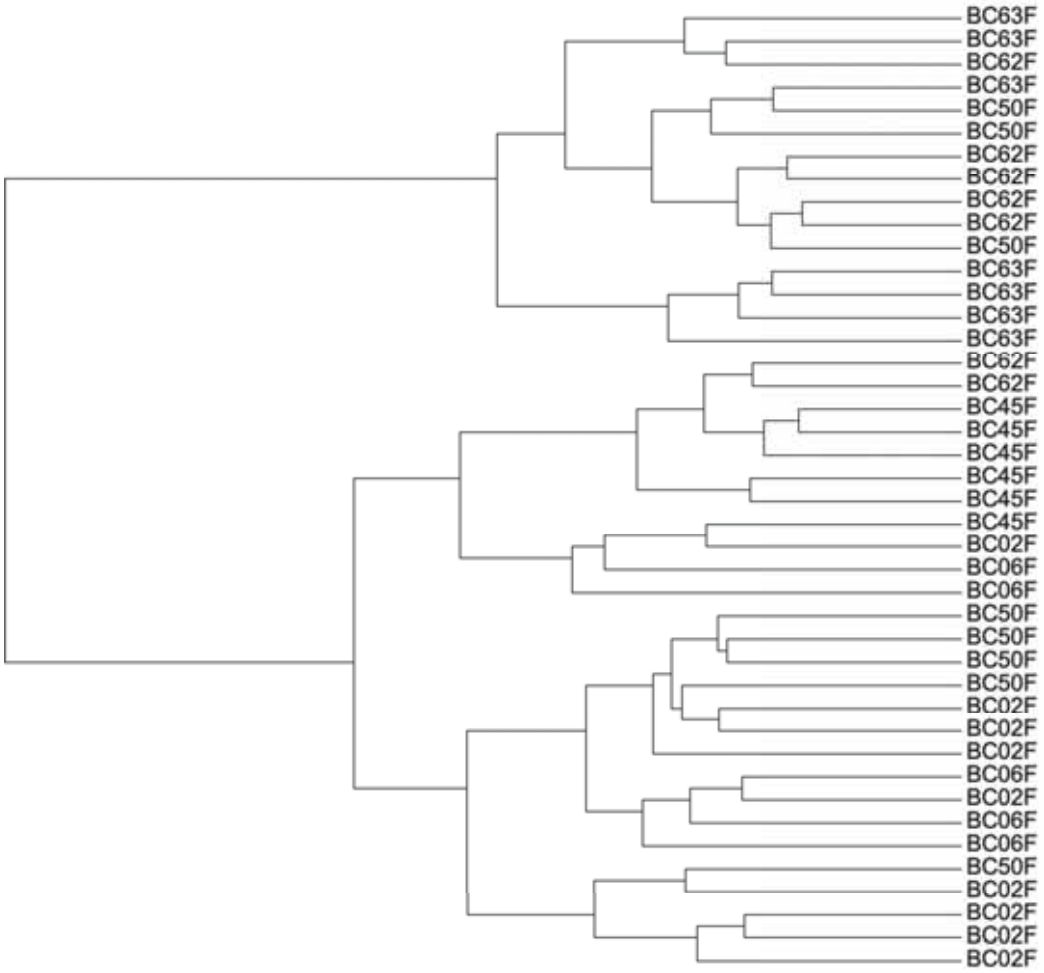
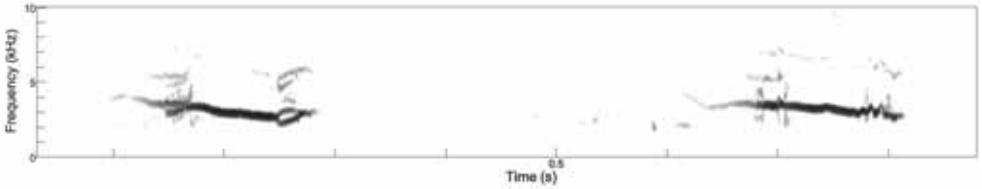
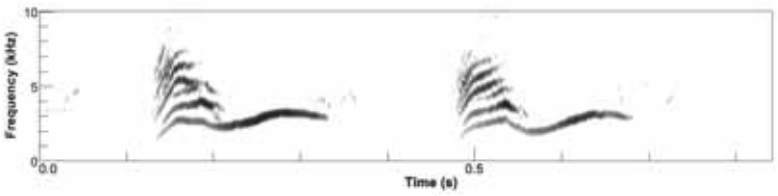


Figure 4.13: Dendrogram of song similarity in 5+ female exemplars taken from 5 *F.teydea* females. Branch depth between pairs equates to song dissimilarity as calculated through the DTW, which is then clustered using Ward's Method. Each branch is labelled by an individual's identifier.

(a)



(b)



(c)

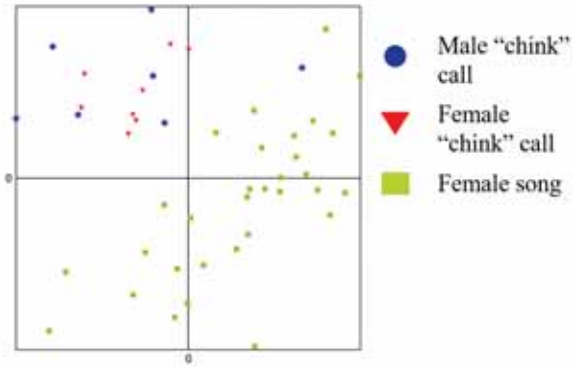


Figure 4.14: a,b - spectrogram of 2 calls produced *F.teydea*. c - NMDS plot from 16 calls taken from both male and female *F.teydea*, and 31 songs produced by females.

F.teydea females produced songs in a non-random manner in relation to other males, regularly overlapping the flourish or pre-flourish syllable (Figure 4.15). In a total of 43 minutes of recordings of 14 naturally singing F.teydea pairs, 96% of female song onsets either overlapped or were produced within 1 second of the end of a male song (15 individuals, male song mean per recording 13.8 ± 4.3, female song per recording = 7.3 ± 2.6). Female song onset occurred on average 0.24 ± 0.61 s before the ending of a male's song (3 cases excluded when a single female produced songs whilst her mate was silent). The proportion of female singing that began either during a male song, or within 1 second of the end, was significantly higher than would be expected by chance (Wilcoxon signed rank test: V = 120, P <0.001, n = means for 15 pairs).

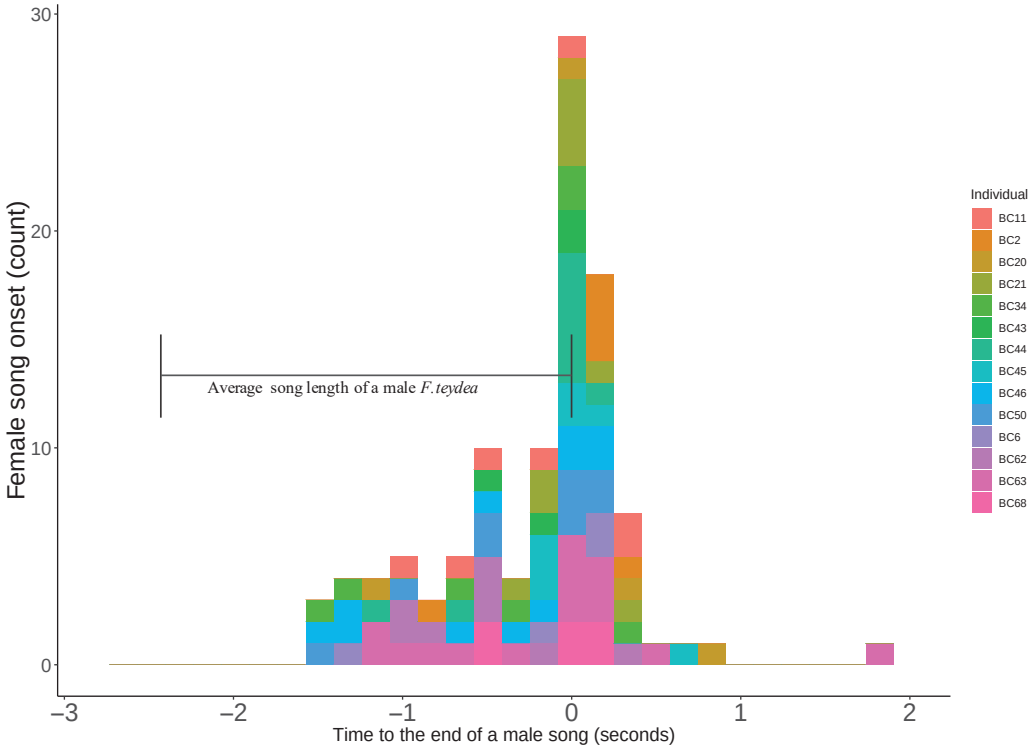


Figure 4.15: Timing of female songs in relation to the end of a male song in 45 minutes of recordings. Each bin is of width 0.15ms. Songs produced greater than 2 seconds after the ending a male song have been excluded from the figure (3/109 songs). Colours highlight individual females.

4.3.2 Playback responses

4.3.2.1 *F.coelebs*

22 individuals (11 territorial breeding pairs) were assessed in how they approached speakers producing female *F.coelebs* song and the control stimuli. Territory owners responded significantly faster to female song than *M.georgiana* (Mdn of pair means *F.coelebs* 48 seconds, *M.georgiana* 360 seconds (i.e. no response), n = 11 pairs, Wilcoxon signed rank test V = 223, p <0.001, Fig 4.16a), and made a significantly closer closest approach (Mdn of pair means *F.coelebs* 4m, *M.georgiana* 20m (i.e. no response), n = 11 pairs, Wilcoxon signed rank test, V = 190, p <0.001, Fig 4.16b). The overall proportional playback score for approach to the female speaker was significantly higher than approaches made to the swamp sparrow speaker (Mdn of pair means *F.coelebs* 5.29, *M.georgiana* 0, n = 11 pairs, Wilcoxon signed rank test V=220, p <0.001., Fig 4.16e), with the time spent within 2m from the speaker (Mdn of pair means *F.coelebs* 3s, *M.georgiana* 0s, n = 11 pairs, Wilcoxon signed rank test, V=0, p <0.05, Fig 4.16c) and the time spent between 2 - 4m of the speaker (Mdn of pair means *F.coelebs* 33s, *M.georgiana* 0s, n = 11 pairs, Wilcoxon signed rank test, V=0, p <0.001, Fig 4.16d), significantly greater if that speaker was broadcasting female song. As a result, under every metric measured, female song induced a response significantly greater than that of a control stimulus in *F.c.canariensis*.

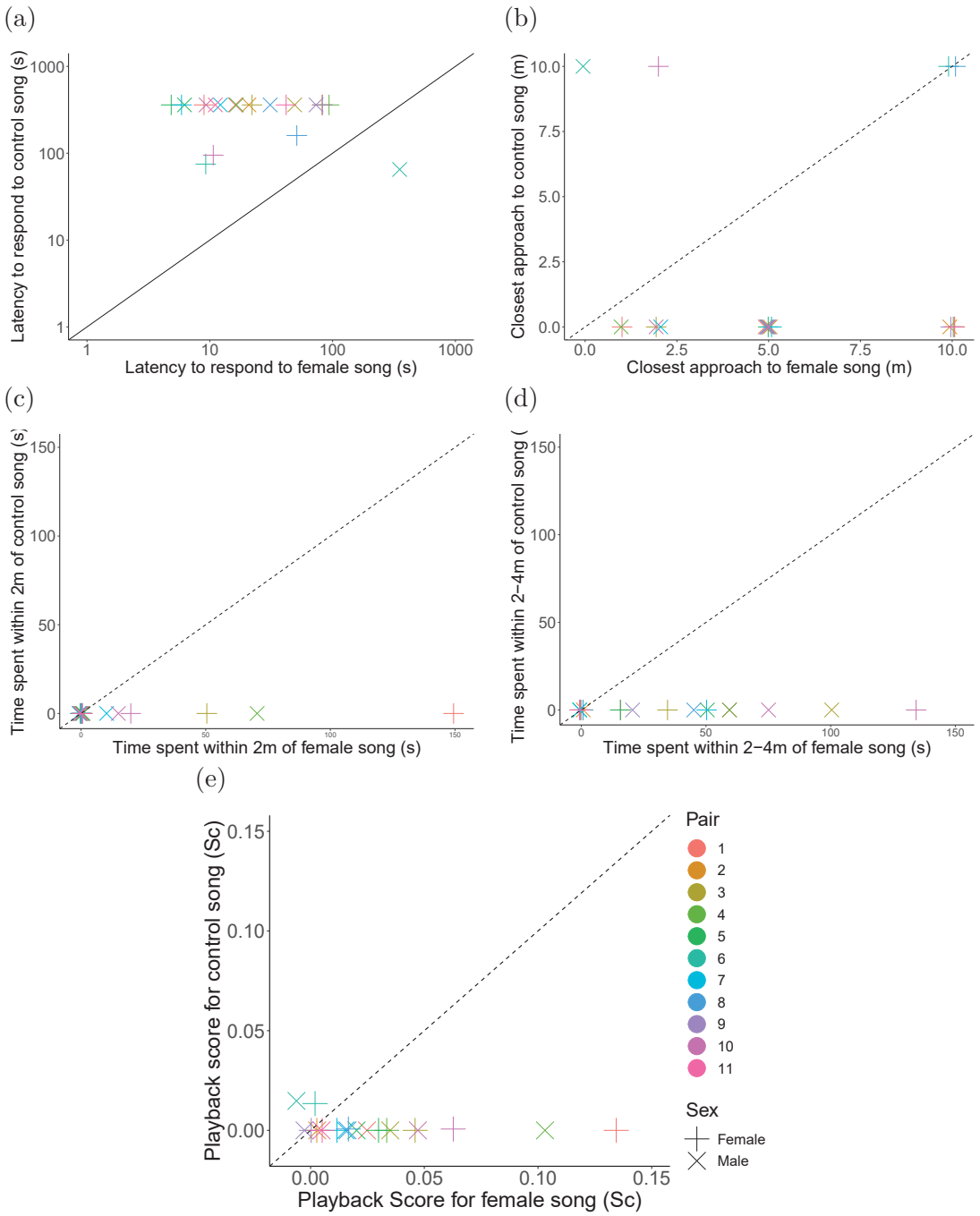


Figure 4.16: 5 response measures (a - latency to make an initial response, b - closest approach distance, c - time within 2m of the speaker, d - time within 2-4m of the speaker, e - playback score) to the playback of control songs and female chaffinch song in 11 breeding pairs of *F.c.canariensis*. Each mark represents an individual, with colours indicating pairings, and the shape indicating the sex of the individual (males x, females +). Individuals which responded equally to both stimuli types would fall along the dotted line (x=y), with points away from the dotted line indicating a bias towards one stimuli. For response metrics b-e, it is thought that a greater number is indicative of a stronger response. For latency to respond, a longer latency is thought to indicate a weaker response.

20 further individuals from 10 breeding pairs were assessed in how they responded to male *F.coelebs* song compared to female. Responses to this playback varied greatly from pair to pair and individual to individual. 7/20 individuals had a greater playback score to female song than male song 4.17e. When considering territorial pairs, latency to approach male song was significantly lower than female song Mdn of pair means, male song = 42 seconds, female song 132 seconds, n = 10 pairs, Wilcoxon signed rank test, V=43.5, p <0.001, 4.18a spent within 2m of the male speaker compared to female (Mdn of pair means, male song = 25 secpnds, female song 0 seconds, n = 10 pairs, Wilcoxon signed rank test, V=150.5, p <0.001, 4.18c). Overall, the proportional playback score was not significantly different between the songs of either sex (Mdn of pair means, male song Sc = 8, female song Sc = 1.33, n = 10 pairs,V=77.5, p >0.3).

When looking at sex specific differences in responses, it was found that males spent significantly longer between 2-4m (male Mdn 30 seconds, female Mdn 5 seconds, n = 10, Wilcoxon signed rank test, V=34, p <0.03, 4.18c) to the female song speaker than females, when presented alongside a control. However, when female song was presented alongside male song, no significant differences for any of the playback metrics were found between the sexes, though response scores by males were generally higher. As an additional anecdote, no female song was produced by territorial females, in response to the playback stimuli.

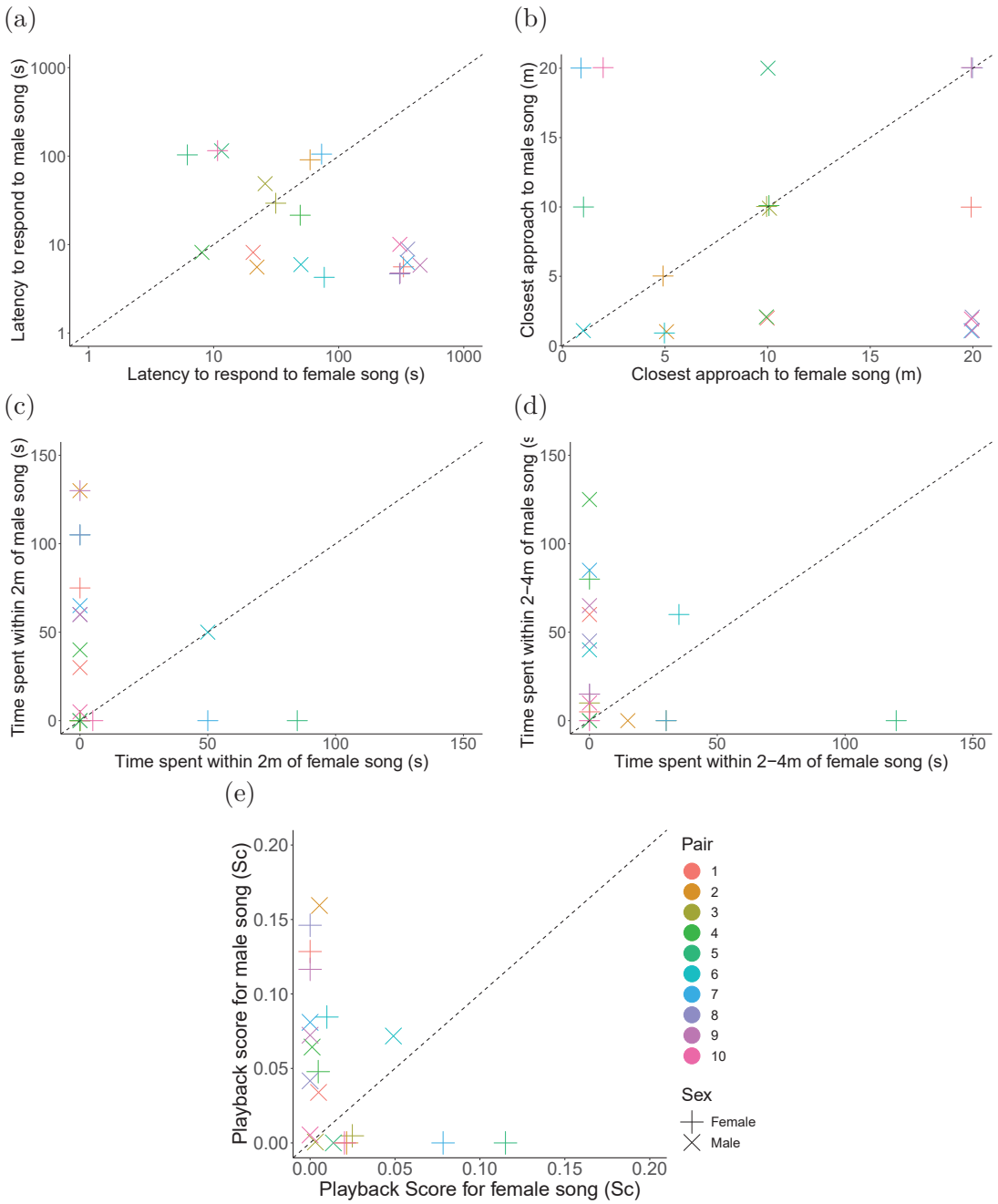


Figure 4.17: 5 response measures (a - latency to respond, b - closest approach distance, c - time within 2m of the speaker, d - time within 2-4m of the speaker, e - playback score) to playback of male and female chaffinch songs from individuals forming 10 breeding pairs. Each point represents an individual bird, with colours indicating birds from the same pair, and point shape the sex of the individual. Cases where an individual responded equally to both stimuli types fall along the dotted line, with points away from the dotted line indicating a bias towards one stimuli.

4.3.2.2 *F.teydea*

8 breeding pairs were assessed in how they approached speakers produced conspecific female and alien heterospecific song. Responses by *F.teydea* to playback of a female song compared to the control echoed the responses by *F.c.canariensis*. Pairs made a significantly quicker approach (Mdn of pair means *F.teydea* 48s, *M.georgiana* 360s (no response), n = 9 pairs, Wilcoxon signed rank test V = 33, p <0.05, Fig 4.18a) and made a significantly lower closest approach (Mdn of pair means, *F.teydea* 4m, *M.georgiana* 20m (no response), n = 9 pairs, Wilcoxon signed rank test V = 3, p <0.05, , Fig 4.18b) to female song than to control song. The proportional approach score was again significantly greater for speakers broadcasting female songs compared to controls (Mdn of pair means, *F.teydea* Sc= 5.25, *M.georgiana* Sc = 0, n = 9 pairs, Wilcoxon signed rank test V = 136, p <0.001, , Fig 4.18e). However, just 3/18 individuals approached within 2m of the speaker for any length of time, and just 6/18 individuals went closer than 4m. Neither of these proximity measures, registered as significant for either sex relative to approaches to the control speaker. In terms of song production, wild females produced song in response to 2/6 duet playbacks, 2/6 male-only playbacks and 1/6 female-only playbacks.

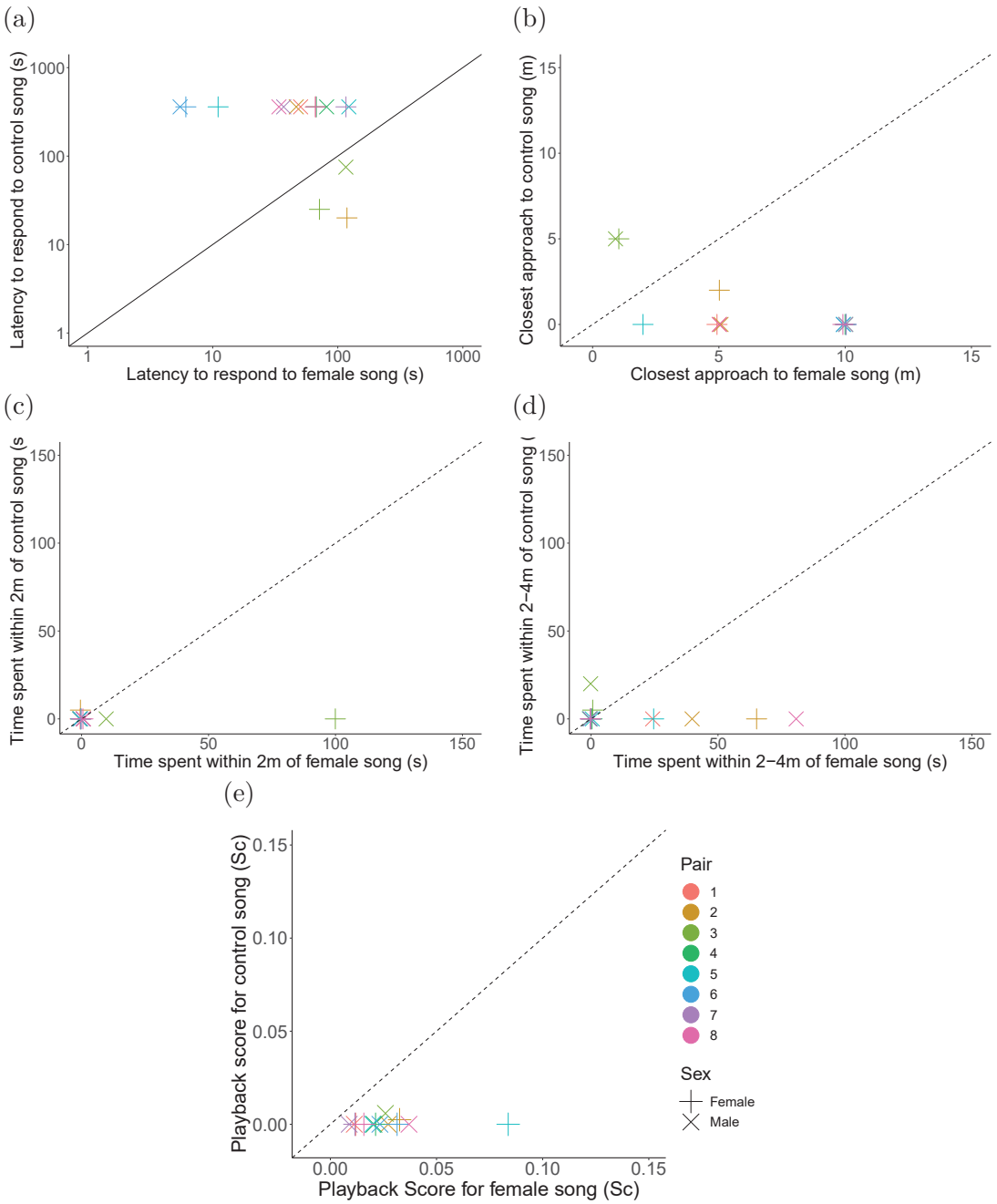


Figure 4.18: 5 response measures (a - latency to respond, b - closest approach distance, c - time within 2m of the speaker, d - time within 2-4m of the speaker, e - playback score) to playback of control stimuli and female blue chaffinch song from individuals from 8 breeding pairs. Each point represents an individual bird, with colours indicating birds from the same pair, and point shape the sex of the individual. Cases where an individual responded equally to both stimuli types fall along the dotted line, with points away from the dotted line indicating a bias towards one stimuli.

4.3.3 Responses to duetting playback

In our duetting experiment, PC1 accounted for 36.85% of the variance in the data over the 2-minutes of active playback. PC1 was loaded negatively for the latency to respond to stimuli and closest approach distance (-0.47 and -0.46 respectively), and positively for time spent between 2m and 2-4m (0.59 and 0.45 respectively). As these were all in line with our expectations for greater response strength, PC1 was used in the MCMCglmm as a response measure. Stimuli type was not found to be significantly associated with PC1 (Figure 4.19). For all fixed effects, only stimuli order (the order through which stimuli were presented) were found to have a significant relationship with PC1 (Table 4.4).

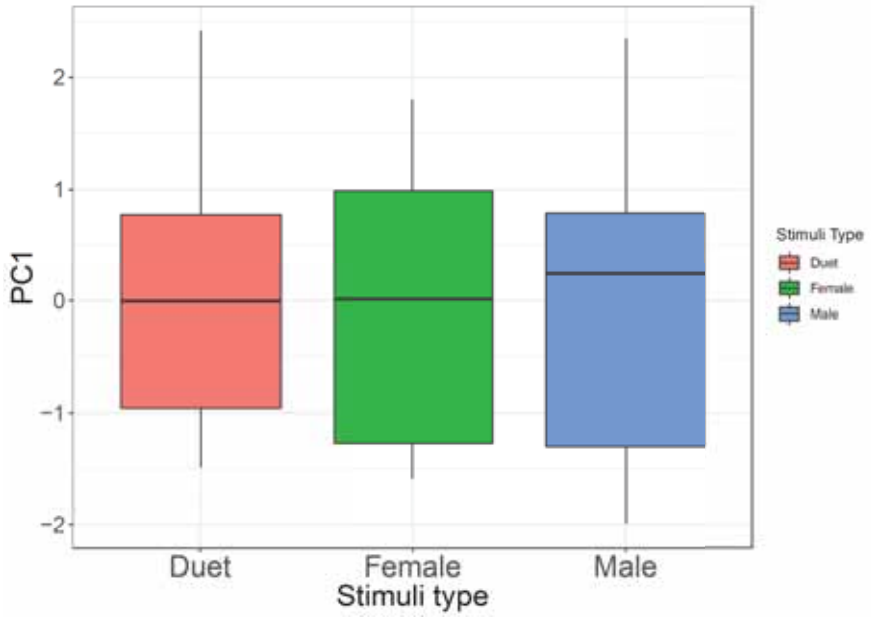


Figure 4.19: PC1 of aggressive responses by territorial *F.teydea* in relation to solo male, solo female and duetting playback stimuli, over the 2 minute trial observations.

Table 4.4: Summary table of the MCMCglmm for the relationship between stimuli attributes and the first principle component of response metrics by territorial individuals

Fixed Effects	Posterior mean	95% credibility interval	Effective Samples	pMCMC
Intercept	0.70	-0.35 - 1.80	8676	0.210
Sex(M)	0.36	-0.75 - 1.44	9000	0.516
Stim(F)	0.11	-0.98 - 1.23	9000	0.843
Stim(M)	-0.48	-1.56 - 0.31	9000	0.370
Order	-0.40	-0.81 - 0.03	8627	0.041*
Sex(M): StimFemale	-0.35	-1.94 - 1.20	9000	0.643
Sex(M): Stim Female	0.69	-0.87 - 2.24	9000	0.376
Random Effect				
Pair	0.07	0.00 -0 .47	315.3	

4.3.4 Year-round territoriality in *F.coelebs*

To test whether territory defence was sustained during the winter in Tenerife, 12 territorial adult males were captured in mist nets and colour ringed during the 2015 & 2016 breeding season. Territories were re-visited on the 15th and 29th December 2016, a point at which we would not typically expect males to occupy their breeding season territory or respond to conspecific playback (Marler, 1956a). In the first visit, all 10 birds were found to be defending their territory, and on the 2nd visit 9/10 were present.

4.4 Discussion

4.4.1 Key findings

Female chaffinches *F.coelebs* and Tenerife blue chaffinches *F.teydea* have not been considered to produce song in the wild (Garamszegi et al., 2007; Kling & Stevenson-Hinde, 1977). In this study, we demonstrated females from 4 subspecies of *F.coelebs* as well as *F.teydea* produce song. In the case of *F.coelebs*, this is the fourth major difference found in the use and learning of song between the Atlantic island chaffinches and those from continental Europe, adding to previous findings by Lynch and Baker (1993) and Lachlan et al. (2013), and those presented in Chapter 3. Female songs were sex-specific, and produced by free-living individuals across the breeding season, though at much lower rates than male song, and often in response to conspecific song. Territorial individuals respond significantly more

to female songs presented through speaker playback, than they would a novel interspecific song, indicating female songs were recognisable as a conspecific signal. Given that I also found evidence for increased territorial value in *F.c.canariensis*, one possible reason for the evolution of this behaviour was to provide territorial defence, similarly to how female song functions in other species (Beletsky, 1983; Cooney & Cockburn, 1995; Hobson & Sealy, 1990; Kriner & Schwabl, 1991; Tobias, Gamarra-Toledo, García-Olaechea, Pulgarin, & Seddon, 2011).

4.4.2 Is it a song?

One of the broader objectives from this study was to identify whether the vocalisations produced by females are indeed songs. As a behaviour, songs are typically differenciated from calls due to factors including acoustic complexity, their nature as a learnt behaviour, sex-specificity and the context in which they are produced (Marler, 2004; Konishi, 1985). Much like the acoustic nature of songs, the exact factors behind what differenciates it from a call, is often species dependant. In the chaffinch, males already possess a sex-specific rain call (Marler, 1956c), and here we present evidence that females produce a vocalisation that is equally as sex-specific. Both the male rain call and the "chink" call have also been previously demonstrated to be subject to learning (Riebel & Slater, 1998a; Nottebohm, 1972a), with juvenile Scottish chaffinches learning Corsican rain calls after tape tutoring (Riebel & Slater, 1998a). Therefore in *F.coelebs*, the key factors seperating the calls from male songs are vocalisation complexity and production context. Male songs contain more syllables and more syllable-types than calls (Marler, 1956c; Nottebohm, 1972a), and are produced in the context of territorial defence or mate attraction (Marler, 1956a, 1956b; Newton, 1964). Under these guidelines, the female *F.coelebs* vocalisations fit more strongly under the confines of what makes a *F.coelebs* song than a call. All female *F.coelebs* songs had more than one syllable, and they often contained more than one syllable-type, ruling out this behaviour being a quickly repeated call, which is common in both sexes across Macaronesia (Kroodsma, 2004). Female songs were also most commonly produced during the dawn chorus, and usually when surrounding chaffinches were singing.

In *F.teydea*, categorising the female vocalisation as a song is a slightly more complex affair. As a less-well researched endemic island species, the extent to which calls are vocally learnt is unknown, and would require more complex testing. In addition, the female vocalisation was largely monosyballic, and no more structurally complex than the *F.teydea* call. Similarly to *F.coelebs*, *F.teydea* female vocalisations are sex-specific, with the only other common sex-specific

vocalisation in the species being the male song. Establishing the context in which female "song" is produced is difficult due to its close association with male song in regards to timing. It might be the case that song is produced in contexts for which males also produce song, or in the context of male song production itself. It is clear though that the timing of song production is different to that of the contact call, which is performed outside of territorial interactions and also by females away from males. The variability in production of female song from individual to individual is another factor which might indicate that song output might be subject to broader environmental conditions. The similarity between the vocalisations of both species (buzziness, rarity, production in the presence of conspecific song) may also serve as evidence that the vocalisations a similar in category.

To summarise, the vocalisations produced by *F.coelebs* females are more resemblent of the male song than any call produced in the species. Whilst *F.teydea* female vocalisations are structurally similar to a call, the contexts of its production alongside male song and sex-exclusivity are more strongly associated with songs. As a result, I consider it safe to conclude that both *F.coelebs* and *F.teydea* sing in wild conditions on the Atlantic Islands.

4.4.3 Intraspecific variability in the presence of female song

This discovery that female song produced exclusively in isolated island populations mirrors findings from Arcese et al. (1988). They reported female song in song sparrows (*Melospiza melodia*) of Mandarte Island, British Columbia, although a much lower proportion of females in their study sang than chaffinches, despite higher observational intensity. The presence of female song in this population was attributed to two potential changes; a mechanistic elevated testosterone level in response to a greater frequency of territorial interactions, and an evolutionary change in how female song could be produced, which in turn might elevate its ability to assist the protection of resources that aid reproductive success. Both of these explanations of Arcese et al. (1988) could also be explored in the Atlantic Island chaffinches.

In regard to increased territorial interactions, population density on the islands was reported to be lower on the islands than in habitats in continental Europe (Dennison, 1991; Lynch & Baker, 1993). However, on the Azores, the density of chaffinches can be as high as 10 pairs per hectare, 10 times greater than that of the mainland (Dennison, 1991). Under these conditions, the frequency of territorial

interactions might be such that female contributions to territorial defence through song production facilitate greater territorial defence success. Given the sequential colonisation of the Atlantic Islands by chaffinches began on the Azores (Suárez et al., 2009), and the lack of evidence of female singing on the mainland (Kling & Stevenson-Hinde, 1977), it is plausible that female singing originated on the Azores. However, this would not explain female song in *F.teydea*, which is thought to have colonised Tenerife directly from Northern Africa (Rando et al., 2010), and for which population density is comparable to mainland *F.coelebs* (Garcia-del Rey & Cresswell, 2005).

For an evolutionary change which could affect production of song, both Atlantic Island *F.coelebs* and *F.teydea*, possess significantly longer beaks than continental *F.coelebs* (García-Del-Rey & Gosler, 2005; Grant, 1979). If this change, which is thought likely to be ecologically driven (Grant, 1979), also corresponded to altered song production which would benefit territorial defence, this might lead to female song in the islands. For example, in the suboscine woodcreepers *Dendrocolaptinae*, species with longer beaks have been found to produce lower frequency vocalisations (Derryberry et al., 2012). A notable acoustic feature of female songs in both *F.coelebs* and *F.teydea* was that they were high in vibrato amplitude (high frequency oscillations or "buzziness"). Male chaffinches also possess buzzy song syllables, in the flourish, and the presence of this phrase has been found to increase the territorial response in playback studies when compared to songs without a flourish (Leitão & Riebel, 2003). Therefore, if longer beaks did assist in producing buzzy songs, and the buzziness of songs correlated with territorial defence, we would expect song to be more likely utilised in subspecies with longer beaks. Currently, the evidence for the impact of beak length on acoustic factors such as trill production is quite mixed (Huber & Podos, 2006), and it would be interesting to see if bill length correlated with the use of buzzier syllables in song in chaffinch males.

One factor to consider in both of these above cases is that both beak length and territorial density is highest on the Azores in *F.coelebs* (Dennison, 1991; Grant, 1979), yet in this study, female song was only observed once in the Azorean subspecies. Though this population was less well studied than *F.c.canariensis* it might be expected that if either of these factors were the primary instigator of female song production, then greater rates of song would have been found on Sao Miguel, than were observed.

In other species, female song also varies in production depending upon the ecology of the subspecies. Baptista et al. (1993) found that the sedentary subspecies

of white-crowned sparrows *Zonotrichia leucophrys nuttalli* sing during the non-breeding season, whilst the migratory *Z.l.oriantha* only produce song when arriving at breeding grounds, often when territorial competition is highest. As a result of singing in winter, Baptista et al. (1993) ruled out changes in androgen levels as the factor behind female singing in *Z.l.nuttalli*, instead attributing female song in both *Z.l.nuttalli* and *Z.l.oriantha* to territorial defence. In the case of this study, observations of chaffinches were restricted to the breeding season. To ascertain whether periodic levels of androgen did result in the production of female songs, hormonal assessment could be made of singing females during the breeding season or future surveying of singing rates during the non-breeding months could be conducted.

4.4.4 The loss or gain of female song

When approaching the question of how female song has evolved in chaffinches, it is initially unclear where there has been a loss or gain of this trait from its ancestral state. Given their larger population size, greater range of habitats occupied, and greater diversity in life history (Marshall, Baker, & Grant, 2013; Carrascal et al., 1992; Ebenman & Nilsson, 1982), it would seem more intuitive to conclude that the continental chaffinches possess the ancestral level of female singing, and the Atlantic Island birds differ from this. One consideration to make here, is that the colonisation of the Atlantic Islands came long before the chaffinches recolonised mainland Europe after the last glacial maximum (Griswold & Baker, 2002; Suárez et al., 2009). In this respect the Canarian population could be considered more ancestral, and therefore female song may have been lost an ancestral capacity to sing, during or following spells in pleistocene refuga.

An alternative method to examine the question of female song ancestary is to look at related species. The chaffinch subfamily, *Fringillinae* comrpises just 4 members, and are distant enough from other finch families to make further exploration useful (Zuccon, Prŷs-Jones, Rasmussen, & Ericson, 2012). Of the four, only the brambling *Fringilla montifringilla*, and Gran Canaria blue chaffinch *Fringilla polatzeki* were not examined in this chapter through field evidence. In the latter's case, its ancestry is extremely likely to be similar to that of *F.teydea*, leaving just *F.montifringilla* as a useful candidate. In their review of female singing in European songbirds, Garamszegi et al. (2007) found no evidence of female bramblings singing. The species is sexually dimorphic and common across Scandinavia and Russia, making it unlikely, though not inconciveable, that female song is common but unreported by field observers (Newton, 1964). The extent of its current range, going as far east as Japan, would make it likely that the species

also occupied multiple pleistocene refugia during glacial maximum events, much like the chaffinch (Blondel & Mourer-Chauviré, 1998). The likelyhood then that a restriction of range or specific biotic charactersitics of refuga led to a loss of song in both *F.coelebs* and *F.montifringilla* is pretty small. In light of this, it would seem most plausible that female song is not ancestral to the *Fringillinae* subfamily.

4.4.5 Evolution of female song

The presence of female song in the Atlantic Islands can be considered to align with prior literature suggesting that rates of female song are higher in species which live in the tropics (Langmore, 1998; Odom et al., 2015, 2014; J. J. Price et al., 2009; Slater & Mann, 2004). When examining New World blackbirds Odom et al. (2015) found strong evidence linking evolutionary changes in life history to the likeyhood of possessing female song. Singing is thought to be ancestral to the oriole clade *Icteridae*, with phylogentic evidence indicating the female song has been lost three times. In each case, this was linked to a change in breeding conditions, where species made historic movements from tropical climates, to temperate ones(Odom et al., 2015). Other factors identified included an absence of seasonality (Odom et al., 2014; Slater & Mann, 2004), stability of monogomous pairings and annual territory residence. In the Icterids, nearly all female singing species occupied territories throughout the year.

The chaffinches on the Atlantic Islands appear to mirror the changes of female song uncovered in the New World blackbirds. The Canary Islands are subtropical in climate and are by far the lowest latitude for which *F.coelebs* breed (Clement, 1999; del Hoyo et al., 2011). The vast majority of chaffinches breed in temperate conditions. As far as I am aware, the island chaffinches provide the first reported instance of a species for which only isolated populations in subtropical habitat have females which sing. Whilst levels of extra-pair copulation have yet to be explored in the Islands chaffinches, in this study we did find evidence of annual territory residence in *F.c.canariensis*.

It has previously been suggested that the New World blackbirds provide an ideal model clade to examine the relationship between female song and life history (Odom et al., 2015). I would make the case that the chaffinches provide a fantastic compliment for studies of this nature. Whilst in one clade, female song learning appears to have been lost due to life history changes, in the other, it appears to have been gained. In addition, chaffinches much like the blackbirds are well understood in terms of their phylogenetic history (Marshall & Baker, 1999;

Marshall et al., 2013) and in *F.coelebs*, also have a species for which there is a greater understanding of song learning and development than known for any New World blackbird. Future research could look to capatilise on this for exploring song development in female chaffinches, potentially through manipulating the environment of native temperate and tropical subspecies and monitoring song development.

4.4.6 Further possibilities on the evolution of female singing

The nature of the Atlantic Islands colonisation and the subsequent evolution in male singing may also relate to the presence of female singing. Male *F.coelebs* have been found to learn song-types less precisely than mainland chaffinches (Lynch & Baker, 1993) and song learnt by the populations have a more relaxed syntactical structure (Lachlan et al., 2013). As part of this thesis, evidence for slower song development in both Atlantic Island *F.coelebs* and *F.teydea* is also presented. If precise, rapid song learning provides males with a more successful signal to defend territories, as would be predicted for chaffinches (Lachlan & Nowicki, 2012; Nowicki, Searcy, & Peters, 2002a; Nowicki, Peters, & Podos, 1998; Slater, 1989), then it might be expected that the Atlantic Island chaffinch males would be less capable at defending territories than continental birds. However, given that precise song learning is rare in the majority of Tenerife (Lachlan, in prep), it would be improbable for female song to compensate for this change directly.

A related suggestion would be that with potentially greater population density (Dennison, 1991) and longer territory ownership, females might need to support males in defending territories by producing their own signal as a defence mechanism. It would therefore be highly useful to ascertain whether the Atlantic Island chaffinches did continue to favour the production of precisely learnt songs, as would be expected of continental chaffinches.

Another possibility is that female song may be another product of the factors which resulted in the evolution of song learning in the island's chaffinch males. The exact cause behind this change remains unclear (Lachlan et al., 2013), and the potential hypotheses relating cultural bottlenecks to changes in male song, are unlikely to be related to newly produced female song, as it requires pre-existing song biases to relax. One suggestion is that an isolated female colonist would be more successful in being found by a male vagrant if they produced song. However, as an explanation for the presence of the behaviour more generally it seems highly unlikely. Females already produce species-specific calls which regularly signal to

distant males (Marler, 1956a). In addition, this cause would likely benefit from the production of longer songs, for which females songs are significantly reduced, particularly in *F.teydea*.

An important consideration to make when exploring hypotheses for how female song became present in the island's chaffinches, is the number of occasions that the behaviour has evolved. It is possible that female song is widespread in chaffinches but is either rarely reported or that only in the Atlantic Islands are the conditions favourable for female singing. Given the wealth of studies which have examined song in chaffinches (Lachlan & Slater, 2003; Marler, 1952; Riebel et al., 2015; Slater & Ince, 1979), and the broad range of habitats occupied by chaffinches across the islands and the rest of their range (Carrascal et al., 1992; Dennison, 1991; Perktaş, Peterson, & Dyer, 2017), these explanations seem unlikely. With Atlantic Islands *F.coelebs* and *F.teydea* both likely to be ancestral to different mainland chaffinch populations (Griswold & Baker, 2002; Rando et al., 2010), it seems most likely that female song has evolved independently on at least two occasions in the Atlantic Islands *Fringillidae*.

It remains uncertain whether the origin of female singing in *F.teydea* is ancestral to its source population, the North African *spodiogenys* and Africana subspecies of *F.coelebs*, found in Morocco, Tunisia and Algeria (del Hoyo et al., 2011). Along with the recently described *harterti* of Northern Libya (L. Svensson, 2015), these populations are also among the lowest latitudes in which chaffinches breed, where they do so in forests or recreational parks in cooler coastal environments. Bioclimatic analysis on habitats used by chaffinch subspecies found significant differences in niche differentiation between North African and European *F.coelebs* (Perktaş et al., 2017). Female song has not been reported in the North African chaffinch subspecies, and no record of vocalisations which match features of female song has yet been uploaded to the online song database Xeno-Canto [www.xeno-canto.org]. However, as these subspecies are far less well studied than the continental chaffinches, this behaviour may well have been previously missed, as was the case with the Atlantic Island chaffinches. Through assessing whether female song is present in the African chaffinches, we can start to unpack the origin of this behaviour, and in turn better understand which ecological conditions have likely driven the evolution of female song in this species, and which may control the presence of female singing in songbird species generally.

4.4.7 The development of female song

The degree of similarity between the songs of males and females is another feature which varies depending on the species. In many, songs or individual syllable types are shared by both sexes (Arcese et al., 1988; Baptista et al., 1993; Farabaugh, Brown, & Veltman, 1988; Wickler & Seibt, 1980). The female chaffinches from Kling and Stevenson-Hinde (1977) which were subject to testosterone implants also developed songs similar to those of males. Yet in this study, females sang sex-specific songs, and there was no indication that males and females shared song components, syntactical structure, repertoire sizes. Riebel (2003) suggested many possible mechanisms for why female and male songs could differentiate, including sex-specific song processing systems, different learning times, restricted vocal development, sex specific differences in learning precision and anatomical inhibitions of vocal output. Of these reasons, the least likely to apply to the Atlantic Island chaffinches relate to developmental changes or interruptions. Songs from females differ substantially from any recorded in the early stages of song development in males. In the studies presented in earlier chapters of this thesis. In addition, unlike developing *F.coelebs*, songs of females *F.coelebs* were highly consistent with successive renditions.

Population-wide song analyses of both continental and British Isles *F.coelebs* (Lachlan & Slater, 2003; Slater et al., 1980) and *F.teydea* males (Lachlan, in prep) have revealed consistent levels of song sharing between individuals. In the Canary Islands, birds learn songs less precisely but do share phrases between individuals (Lynch and Baker (1993) Lachlan, in prep). In this study, we found no evidence that song-types were shared between females, whilst rates of song dissimilarity between female *F.teydea* was similar between geographically close and distant individuals. The lack of evidence for female songs being copied, points towards the potential for sex-specific lineages. There is limited data of other species which might possess this trait (Riebel, 2003). The Bay wren *Thryothorus nigricapillis*, learns songs specific to their sex also, but a tape tutor study by (Levin, 1996) revealed that both sexes can learn components of the other. Such a study may also be necessary to infer the selectivity of song learning in female *F.coelebs*. In addition, further sampling would further clarify whether females are copying other individuals with their song, and that in this study, song copying was missed due to sample size.

4.4.8 The function of female song in *F.coelebs* and *F.teydea*

Female song has been demonstrated to have a broad number of primary functions across songbird taxa (Langmore, 1998), and a key feature of this study was trying to ascertain which of these, if any, applied to the Atlantic Islands *Fringillidae*. For example, one use of female song is for guarding their mate from extra-pair copulations with other females, as found in the Tropical boubou *Lanarius aethiopicus* (Grafe & Bitz, 2004) and the warbling antbird (Seddon & Tobias, 2005). Mate guarding is unlikely to be the primary functon of female song in *F.coelebs*, as in the playback experiments, females responded equivalently to both male and female songs, and no female responded to playback stimuli with song. In addition, unpaired females were recorded as being the most consistent producers of song, in individuals visited on multiple occasions. In *F.teydea*, mate guarding as a function of song remains plausible, especially when considering the consistency through which females produced songs in the presence of the male. In our playback trials, comparable numbers of female song recordings were made when presenting territorial females with male-only stimuli, which might suggest otherwise.

Another potential function for female song would be mate acquisition, in a similar vein to songs produced by female European Accentor species (Langmore, 1998). Several song production attributes make this seem less likely to be the case in the Atlantic Islands *Fringillidae*. Firstly, in *F.coelebs*, female song was only recorded in one individual during February and March, which would be the time period when song displays, as a means of mate attraction, would be expected to be at their highest (Hanski & Laurila, 1993). Song production in both species, but especially *F.teydea*, were also regularly produced following hearing songs from other conspecifics. If songs were used for mate attraction, a greater degree of independent signalling would be expected, as found in the singing males.

Findings from the playback studies support the idea that female songs are used to assist in territorial interactions. Both males and females made close approaches to a playback speaker producing female song, with these behaviours consistently demonstrated as valid measures of strong territorial reaction to male song in both *F.coelebs* and *F.teydea* (Brumm & Ritschard, 2011; Pickstock & Krebs, 1980; Reed, 1982; Slater & Catchpole, 1990). Similar conclusions were also drawn from studies of female song in other species, including comparable rare female song in both *M.melodia* (Arcese et al., 1988) and the yellow warbler *Dendroica petechia* (Hobson & Sealy, 1990), more regular female singers such as the European Robin *Etrithacus rubecula*, the Superb-Fairy Wren *Malurus cyaneus* (Cooney & Cockburn, 1995)

and stripe-headed sparrows *Peucaea ruficauda* (Illes & Yunes-Jimenez, 2008), as well as duetting species such as *Thryothous nigricapillis* (Levin, 1996)

When examining how territorial individuals responded to the production of male and female song simultaneously, pairs would initially fly in between both speakers, before spending a greater period of time with one stimuli, which was more often the male song. This would be consistent with the idea that male and female songs possess similar functions in terms of territorial defence, but that the male is the more aggressive stimuli. Greater male aggression from both male and female song stimuli, has been reported in other playback studies of female singing species, such as the white-bellied antbird *Myrmeciza longipes* (Fedy & Stutchbury, 2005).

Alternatively, female and male song may be being responded to independently for different functions, in ways which are more subtle than can be detected through the playback studies conducted. As an example, even if female song was being used for mate attraction, a male may still approach a male song more than that of a female. To test whether this might be the case, song production by females could be measured in relation to the breeding cycle, with evidence of production after hatching, or during the non-breeding season, likely to rule out mate attraction as a primary function of female song, as found in the *E.rubeluca* (Kriner & Schwabl, 1991).

One feature of previous playback studies on *Fringillidae* species, is that those conducted on wild individuals (Brumm & Ritschard, 2011; Leitão & Riebel, 2003; Pickstock & Krebs, 1980; Slater & Catchpole, 1990), were exclusively on males. Thus, the playback studies presented here are novel in that they also included how females responded to the playback. Though this would require further investigation, females are generally not considered to be an aggressive sex in continental chaffinches, though there may be short time periods during the breeding season in which they do respond to speaker playback (Lachlan, pers comm). Given the finding of sustained territory ownership in the islands chaffinches compared to continental birds, further comparative playback studies conducted during the non-breeding season could help infer whether females are more aggressive to territorial invaders than on the continent. This would again provide further evidence for greater investment in territorial defence by islands chaffinch females.

4.4.9 Duetting

In *F.teydea* we found consistent evidence of a timing bias in female singing, with its production linked to the ending of a male song. Males were the instigator of

song production, with females occasionally giving an instant reply, as found in the Eastern whipbird (Watson, 1969). According to the categories of duetting established by Hall (2009), *F.teydea* would fit into the song co-ordination group of duetting species, much like the "loose" duets found in the Banded wren *Thryophilus pleurostictus* (Hall et al., 2015). In this species, the timing of songs produced by females was also highly variable in their timing in relation to male song, with 38% of female songs were "answers" to male song (either overlapping or within 1s of the end of a male song). Comparable measures used on duetting song bouts in *F.teydea* revealed answering song rates greater than 97%. Therefore, whilst the exact co-ordination between male and females was low, and female song rates were also lower than males, the high degree for which female songs were timed with the ending of the male song would place *F.teydea* as a duetting species.

The current best-guess estimate is that between 3 and 4% of species worldwide produce a form of vocal duet (Hall, 2009). In the Western Palearctic region (Europe, North Africa & the Middle East), duetting is rare in passerines and more commonly associated with non-passerines, such as the drumming of woodpeckers or hooting of owls (Malacarne, Cucco, & Camanni, 1991). Malacarne et al. (1991) examined the relationship between life-history and duetting in these non-passerines and found links with the behaviour and higher rates of territoriality and monogomy. Benedict (2008) similarly examined the North American passerines, running comparitive analyses in 300 species from 31 different families. She found that the behaviour was found in 12 distinct families, and that shifts to long-term monogomy and longer territory ownership were more strongly associated with gains of duetting. In this study, we found that *F.c.canariensis* held its territory permanently, but did not investigate this in the duetting *F.teydea*, nor rates of extra-pair copulation. Attempts to conduct this research in future, could help align the presence of duetting in *F.teydea* with other duetting birds.

Meta-analyses has also been used to identify the main functions of duets. Dahlin and Benedict (2014) concluded that they are usually a multifunctional behaviour, with the most likely function to be joint resource defence. For individual species, playback is a primary method used to assess whether this is the case (Fedy & Stutchbury, 2005; Hall, 2000; Koloff & Mennill, 2011, 2013; Mennill, 2006; Hathcock & Benedict, 2018). Female canyon wrens *Catherpes mexicanus* also produce rare songs (Hathcock & Benedict, 2018). Using a playback method involving either presenting alternating or overlapping male and female songs,Hathcock and Benedict (2018) revealed that females would respond similarly to both types of stimuli, but rates of duetting were not higher when presented with duetting stimuli. Whilst this result is similar to those presented in my duetting study, female

F.teydea rarely ever produced solo songs, meaning that it cannot be concluded that female-solo song is highly functional.

F.teydea was more similar in its response to duet and solo song with the white-bellied antbird *Myrmeciza longipes* (Fedy & Stutchbury, 2005). Fedy and Stutchbury (2005) concluded that no increase in response to duetting would be predicted to occur when combined signalling serves non-territorial functions, such as within-pair communication or mate guarding (Fedy & Stutchbury, 2005; Langmore, 1998; Sonnenschein & Reyer, 1983). In Hall et al. (2015), rates of female singing were investigated over time to reveal the primary function of duetting in partner communication, as well as a secondary function in territorial defence. A similar examination would help ascertain, the function, if any, duetting has in *F.teydea*.

4.5 Summary

I investigated evidence that two species of *Fringillidae* have females which produce song, which in the case of *F.coelebs* is different from the rest of its range. Females from 4 different subspecies of *F.coelebs* and *F.teydea* were recorded producing songs. These were produced less often than males would sing and the songs shared few acoustic characteristics, which may be as a consequence of a more limited, or alternative song development pathway to males. In *F.teydea*, nearly all songs by females are as part of a loose duet with a surrounding male, a behaviour more common in tropical, annual territory holding species. In *F.coelebs*, female singing is the fourth major evolution in song learning which differs in the Atlantic Island populations, along with males developing songs more slowly (see Chapter 3), with less precision (Lynch & Baker, 1993) and with more relaxed syntactical structure (Lachlan et al., 2013) than continental birds. When examining the evidence, it seems more likely that female song is more ikely to be a product of environmental conditions of the Atlantic Islands, rather than as a product of colonisation. The chaffinches could serve as a good partner alongside clades such as the New World blackbirds for further investigation into female song. Future examinations of female song in the chaffinches should look to identify if the behaviour is produced throughout the year, and whether other peripheral chaffinch populations, such as those in North Africa. More broadly, a detailed examination into the song development of male and female individuals of the same species could help shed further light on the processes and evolution of vocal learning.

Chapter 5

Discrimination between complete and recombined songs in island and mainland chaffinch populations

Abstract

The chaffinches of the Atlantic Islands learn songs less precisely than their relatives in continental Europe, in particular recombining syllables from multiple tutor songs rather than learning whole songs. But we still have little understanding of what evolutionary processes have caused this. Three possible explanations for the island birds' behaviour include: (a) the cost of learning precisely has increased; (b) that learning novel songs may have become adaptive due to a change in song preferences, or (c) that the signal of quality generated through imitating a song precisely might be reduced due to reduced sexual selection. Here, these hypotheses were tested through conducting a song playback experiment in three *F.coelebs* populations differing in levels of learning precision: mainland Spain, the Azores, and Tenerife. Territorial males were presented with alternating song stimuli, built from syllables from other local males. Song stimuli were either intact copies of real songs or recombined to form novel songs. Two response measures were derived from the approaches made by a territorial male towards a speaker, and the relationship between stimuli type and response measures tested through a series of nested LMMs. Limited evidence was found for a link between the precision of song and how aggressively they would respond to intact songs compared to recombined

ones. Low precision learning Tenerife chaffinches had similar responses for both stimuli types, while high precision mainland birds responded more aggressively to intact songs. The impact of order effects in the experimental design utilised meant that though findings suggest that selection for precise song learning has weakened for the Atlantic Islands chaffinches, further testing on both male and female song preferences would be required to confirm this.

5.1 Introduction

Common chaffinches *Fringilla coelebs* learn their songs extremely precisely, imitating entire song-types in full and retaining the sequence order song syllables were sung in (Lachlan & Slater, 2003; Marler, 1956c). Whilst the Atlantic Islands chaffinches retain precise learning of individual syllable-types (Lachlan et al., 2013; Lynch & Baker, 1993), strings of syllable sequences are much more diverse in the islands than in continental Europe (Lachlan et al., 2013; Lynch & Baker, 1993). This difference, combined with a relaxed syntactical structure and increased repertoire size in island populations, has been proposed as resulting from genetic evolution in song learning behaviour (Riebel et al., 2015). However, the consequences of such imprecise learning on communication remains open to question.

Whilst precise learning of phrases and phrase transitions is the norm for continental chaffinches, this is not always the case in other species. In the zebra finch *Taeniopygia guttata* (Eales, 1985), males also learn their songs from tutors, and females have been demonstrated to preferentially select males with well-learned song (Holveck et al., 2008) or more complex song structures (Clayton, 1989). However, in practise, males often use different introductory syllables and may not precisely replicate syllable transitions of a tutored model (Holveck et al., 2008; Mann & Slater, 1995). Nightingales, *Luscinia megarhynochos* were also found to learn songs from tape tutors, but subsequently sing those components in a different order (Hultsch & Todt, 1989), including in subsequent renditions (Hultsch & Todt, 1996). Intraspecies variation in song learning precision can also be found in the song sparrow *Melospiza melodia*. The western population learn song-types fully, and utilises those in song-type and repertoire matching contests with territorial neighbours (Beecher, Stoddard, Campbell, & Horning, 1996). A population in Pennsylvania on the other hand showed little evidence of sharing full song-types, and instead matched parts of songs (e.g. trills or note complexes) they shared with neighbours (Hughes et al., 1998). Thus, there is a precedent for species to differ in how precisely they learn song and examining such divergence in

closely related taxa may allow us to understand the factors shaping the evolution of learning.

To further examine why island chaffinches learn songs with low precision, the driving mechanisms behind high song learning precision in the continental and British chaffinches need to be understood. Many of the proposed reasons for precise learning focus on interactions with neighbours and matching to the local habitat (Beecher & Brenowitz, 2005; Nottebohm, 1970). These seem less plausible for European chaffinches as they seldom learn songs from direct territorial neighbours (Lachlan & Slater, 2003), and there is little evidence of song adaptation in relation to territory habitat (Williams & Slater, 1993).

An alternative explanation for precise learning in chaffinches is through serving as an honest signal of early-life conditions (Lachlan & Nowicki, 2012; Nowicki, Searcy, & Peters, 2002a; Nowicki et al., 1998). Under this hypothesis, young songbirds that experience stress during a key period of physical development, would continue to signal this later in life, through discriminable features of their song (Nowicki, Searcy, & Peters, 2002a). Developmental stress has been found to impact how precisely songbird yearlings develop song in a number of ways, including reduced song and song component complexity (Müller, Vergauwen, & Eens, 2010; Spencer, Buchanan, Goldsmith, & Catchpole, 2003), song learning accuracy (Nowicki, Searcy, & Peters, 2002a), repertoire size (Schmidt, MacDougall-Shackleton, Kubli, & MacDougall-Shackleton, 2014), song performance (Buchanan, Spencer, Goldsmith, & Catchpole, 2003), the acquisition of song syntax and song learning precision (Holveck et al., 2008) and time spent during stages of song development (Nowicki, Searcy, & Peters, 2002a). It is then hypothesised that these weaker song signals, can then serve a selective function through discrimination by conspecifics (Buchanan et al., 2003; Spencer et al., 2003; Woodgate, Bennett, Leitner, Catchpole, & Buchanan, 2010).

One method of examining song discrimination is through speaker playback studies. Songs are broadcast from a speaker positioned within a territory, and the responses of the territory owner are measured (Kroodsma, 1986; McGregor, 2000). These typically include the closeness an individual engages the speaker (Brindley, 1991; Leitão & Riebel, 2003) and time it spends close to the speaker (Brindley, 1991; Burt et al., 2001; McArthur, Peters, Searcy, & Marler, 1981; Mennill, 2006; Slater & Catchpole, 1990). In some species, such as willow warblers *Phylloscopus trochilus* and great reed warblers *Acrocephalus arundinaceus* responses are more intense to songs which are thought to be discriminated against (Catchpole, 1981; Järvi, Radesäter, & Jakobsson, 1980). In these instances, it was considered that

birds are reticent to engage in a conflict with a threatening signal. In other species, including the chaffinch, a close approach is considered to correlate with a stronger signal (Brindley, 1991; Lachlan, Anderson, Peters, Searcy, & Nowicki, 2014; Leitão & Riebel, 2003; Leitão, Ten Cate, & Riebel, 2006; Reed, 1982; Slater & Catchpole, 1990), on the basis that the owners mediate their reaction based upon the threat to their territory from a signaller. Though determining whether a strong response is induced by a strong or weak signal requires additional evidence, demonstrations that individuals respond differently to categories of signal, indicate that differences within the categories are salient to territory holders (Searcy & Beecher, 2009).

Through playback studies in captivity, female song sparrows *Melospiza melodia* (Nowicki, Searcy, & Peters, 2002b) and zebra finches *Taeniopygia guttata* (Spencer et al., 2005) were assessed in how they responded to developmentally stressed males. In both species, females discriminated against songs produced by males which had undergone developmental stress. Further research in swamp sparrows *Melospiza georgiana* found that both males and females discriminate against songs which are less typical versions of that particular song-type (Lachlan et al., 2014). In chaffinches, studies examining the degree of selection against well-learnt and less well-learnt song have been limited (Riebel et al., 2015). This is in part due to the difficulty in assessing female preferences, as they are by nature inconspicuous and reticent to approach songs from speaker playbacks (Riebel & Slater, 1998b). An operant conditioning experiment by Riebel and Slater (1998b) on captive female chaffinches investigated how they would respond to a song they either recognised or was alien to them. Females responded similarly regardless of which song was presented. A second study compared how females responded to songs which were complete or lacked the terminal flourish phrase Riebel and Slater (1998b). In this instance, females were in general, found to discriminate against the incomplete songs. Later, Leitão et al. (2006) presented captive females with chaffinch songs with different numbers of trill phrases, for which songs with greater phrase numbers were responded to more strongly.

A more common approach for assessing song quality utilises responses made by males, which can be conducted in the wild in predominantly male singing species, such as the chaffinch. Leitão and Riebel (2003) also examined the responses of male chaffinches to songs with differing numbers of trill phrases, and found the males behaved similarly to the females and responded more strongly to more complex songs. In a similar study, males also replicated the behaviour of females in responding more strongly to songs which possess a flourish phrase, to songs with the flourish absent (Leitão & Riebel, 2003). In regard to the Atlantic Island chaffinches, Slater and Catchpole (1990) found that the Tenerife subspecies *F.c.canariensis*,

respond more strongly to songs from their own population, compared to songs produced by a British chaffinch. This indicated *F.c.canariensis* birds were still able to process which song was more threatening despite any two individuals rarely learning the same song (Lynch & Baker, 1993).

One potential explanation for the loss of precise song learning on the islands is that this form of learning has become too energetically costly (although the potential costs of precise learning are not well understood). This might occur if physical or biotic characteristics of the island impact the transmission of song (M. C. Baker, 2006; Slabbekoorn & Smith, 2002b). Alternatively, changes in breeding timings could result in the birds' sensitive phase of song development being less well aligned to song production in adults, inhibiting the capability of yearlings to memorise song models (Nottebohm, 1968). In these instances, as the ability of the bird to produce songs precisely is the limiting factor, we would expect the Atlantic Island birds to retain a stronger response to well-learned song compared to less-precisely learned song.

On the other hand, song change may be driven by an evolution in song preferences. For example, it is thought that a reduction in genetic diversity which coincides with a limited population capacity (Frankham, 1997), can lead to less variance in male quality (Brown, 1997; Morinay et al., 2013) With less variance in the population, the value in the assessment of song quality might be lowered to the extent where it reduces inter-sexual selection (Brown, 1997). Such arguments are supported through findings of reduced extra-pair paternity rates (Griffith et al., 1999) and parental investment (Covas, 2011) in species living on islands. In the islands' chaffinches these rates are not known, but when examined by A. J. Baker et al. (1990), evidence for a strong genetic bottleneck was limited to just one Atlantic Island chaffinch population, El Hierro.

Another possibility is that small founder population sizes accentuate the effect of cultural drift, potentially resulting in a song "bottleneck" (Rendell et al., 2011). In its most extreme theoretical case, young colonists which lack fully developed song, may instead resemble isolate-reared birds if they are unable to contact potential tutors (Thielcke, 1973). As a result, the smaller founder population may quickly lose song components present in their source population (Harbison et al., 1999). Cultural drift can then be exacerbated by sexual selection, resulting in rapid innovations and new song components (M. C. Baker, Baker, & Baker, 2003; Rendell et al., 2011; Searcy, 1992b). Under the "cultural trap" hypothesis, less restrictive learning biases can evolve under conditions of high drift, when receivers attempt to distinguish songs produced by conspecifics and the goal for signallers is

produce songs which are recognisable (Lachlan & Feldman, 2003) If a relaxation in song preferences has occurred, then it would be expected that islands' chaffinches would respond equally to precise and less precisely learnt songs.

A third hypothesis is that island chaffinches may instead have evolved preferences for more innovative and individually distinctive songs. Whilst direct preferences for novelty have not yet been found in songbirds, preferences for diverse, large repertoires have (Byers & Kroodsma, 2009; Nowicki, Hasselquist, Bensch, & Peters, 2000), and it is plausible that innovation could aid the development of a larger repertoire. This hypothesis argues that innovative phase sequences could serve as newly evolved signal of quality in the islands' chaffinches. In this case, a male possessing innovative songs would trigger a stronger defensive response when invading a rival males' territory than a precisely learnt song.

To examine why song learning precision is lower in the Atlantic Island chaffinches, a series of playback studies were ran in several chaffinch populations. Free-living males were presented with 2 song conditions; one a copy of a full song-types they would recognise (intact), and one with recognised phrases which were artificially combined to form a novel song-type (recombined). Stronger responses were considered indicative of a more aggressive and powerful song signal, in line with the evidence from previous playback studies on chaffinches (Leitão & Riebel, 2003; Leitão et al., 2006; Reed, 1982; Slater & Catchpole, 1990).

Three hypotheses are considered for the level of discrimination chaffinches exhibit against intact songs relative to recombined. In all three hypotheses, it is predicted that birds from a continental chaffinch population, which learn songs precisely, will respond more strongly to intact stimuli compared to recombined. The hypotheses differ in regard to the discrimination displayed in the Atlantic Island chaffinches. In the first hypothesis, which considers that the conditions for song learning have changed on the islands, receivers will also exhibit stronger responses for intact songs. In the second hypothesis, that receivers no longer prefer precisely learnt song, predicts that similar responses would occur from the playing of either an intact or recombined song. The third hypothesis, that island chaffinches have evolved preferences for innovative songs, predicts that island birds will respond more strongly to the recombined songs.

5.2 Methods

5.2.1 Song collection

We examined 3 *F.coelebs* populations to take advantage of the sequential nature of decreases in learning precision present in the Atlantic Islands chaffinches (Lynch & Baker, 1993). The precise learning population *F.c.coelebs* was from Catalunya, Spain. The second was in São Miguel, the Azores, *F.c.moreletti*, one of the first islands colonised by chaffinches in the Atlantic (Griswold & Baker, 2002; Marshall & Baker, 1999). Here, chaffinch songs heard in passing might resemble those of continental birds, but tend to sound slightly "simpler" (Marler & Boatman, 1951). On closer inspection, few birds ever produce the same song type indicating a high level of mutation in learning complete song-types (Lynch & Baker, 1994). The third population on Tenerife *F.c.canariensis*, was one of the last to be colonised by chaffinches in the Atlantic Islands (Marshall & Baker, 1999). Chaffinches here regularly perform songs that contain very little by way of syntactical structure, and have highly variable syllable numbers per song (Lynch & Baker, 1994).

To construct playback stimuli song recordings were collected from wild males between 20 minutes before sunrise and 1200hrs. Song recordings were made with a TASCAM -DR100 MkII and Telinga Pro-8 Twin Science Microphone set within a Telinga parabola of diameter 570mm. Recordings were digitized at a sample rate of 44.1 kHZ onto a SanDisk USB soundcard. At least 40 song recordings were collected for each source individual, and when recording it was noted whether they produced more than a single song type. Only individuals where 2 exemplar recordings were obtained for at least 2 song types had songs utilised for playback study. Chaffinch territory boundaries were assessed and identified during these recording spells, and the number of neighbouring individuals and access to neighbour individual territories was also assessed. GPS recordings were taken from the centre of the source individual territory.

5.2.2 Playback stimuli

I used a repeated measures, single speaker design in this playback study. Each stimulus set was formed by selecting 4 previously unused source song recordings; 2 songs from one song type and 2 from another (Figure 5.1). Acoustic manipulation of songs was carried out with the Audacity software package (audacity.sorceforge.net). Each song was transformed using a high-pass filter (800 Hz, 6dB roll off), to remove low frequency background noise, and normalised for amplitude (3dB). Songs were then split into two at the phrase boundary (the transition from one set

of repeated syllables to another) closest to the centre of the song. This resulted in 8 song halves per source individual (Figure 5.1). These were then placed together in particular combinations, such that each fragment was equally represented in 2 different types of stimuli; “intact”, where syllables are presented in the order they were recorded in, and “recombined”, where the first half of the syllables were from one song-type and the second half from another.

2 stimuli sets were created for each set of 4 source songs, with 1 set beginning with an intact song, and the other a recombined song in a counterbalanced design (Figure 5.1). Each song was played 12 times in a row over a 2-minute period (1 song per 10 seconds), designed to reflect the relative song rate of male *F.coelebs* in nature. Songs would alternate between intact and recombined as the playback progressed, with one stimuli set of a given pair playing songs in the reverse order of the other pair.

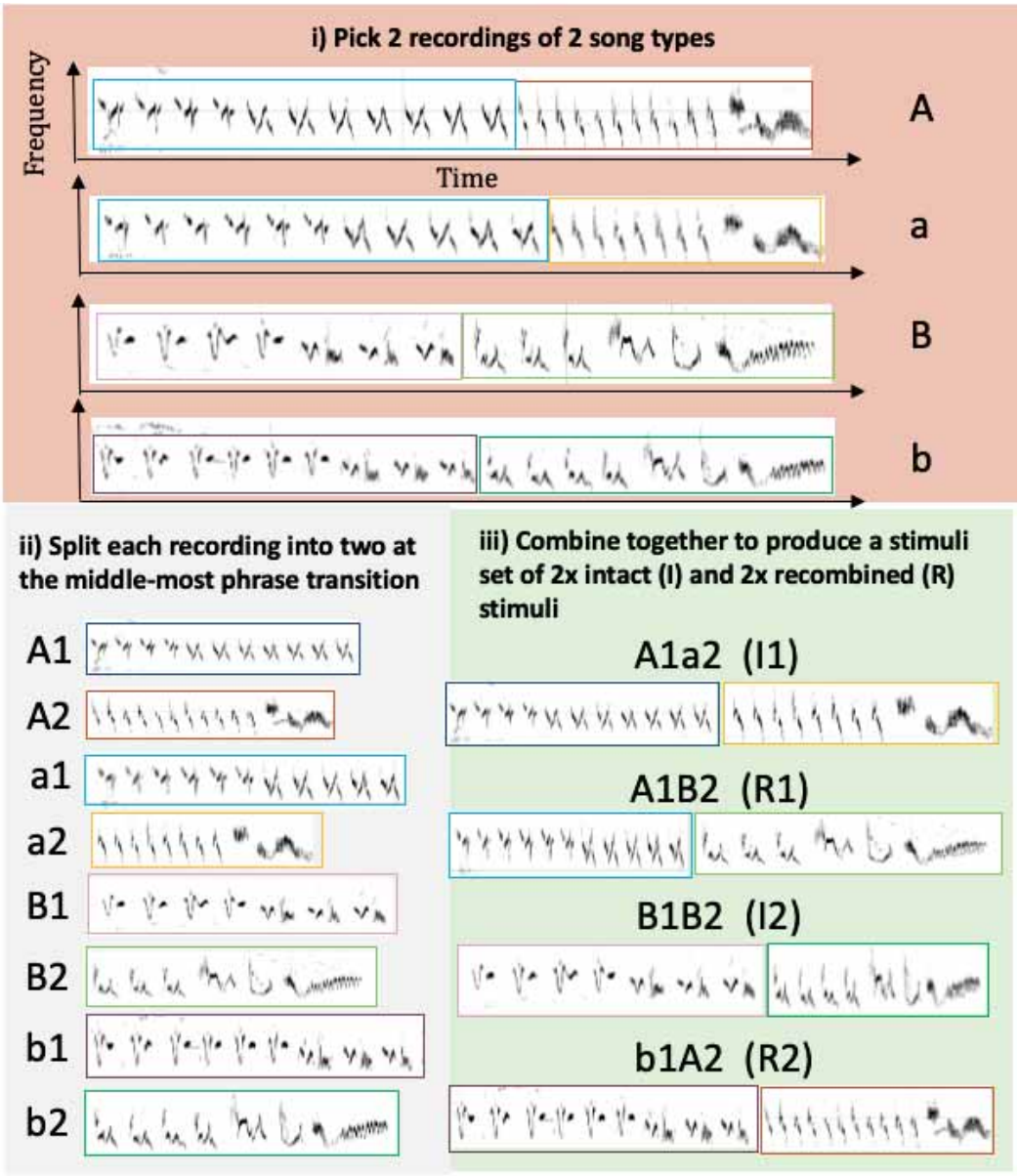


Figure 5.1: Outline of the playback stimuli creation procedure. i) 2 recordings each of 2 different song types were split into 8 song fragments (ii), highlighted here in uniquely coloured boxes. iii) These were then joined together such that each song fragment was only presented once, and either formed part of an Intact stimulus which matched the original example song type, or a Recombined stimulus which was a combination of the two original song types.

5.2.3 Playback protocol

In order to ensure that populations were studied at similar points in their breeding seasons, trials were carried out in Catalunya by Robert Lachlan and in Tenerife and the Azores by Joe Cooper: playback protocol was agreed beforehand, and pilot playback studies carried out by both observers together. Stimuli sets were presented to previously untested territorial males *F.coelebs* between 07:45hrs and

1200hrs on non-windy, non-rainy days. Before trials began, precautions were taken to ensure chaffinches would have genuinely been familiar to the intact song-type they were presented with. In Catalunya, song types can be shared at distances over 30km, and there is little geographic structure within 10km (Lachlan and Mansfield, in prep). Therefore, the songs were presented to random territorial individuals within a 5km range of where they were recorded. In the Azores and Tenerife, the post-juvenile dispersal of birds is less known and reduced song learning precision means that song-types are at best extremely localised, and often exclusive to one individual. Therefore, to guarantee that playback subjects would have interacted with the known song type, these tests were performed on the territorial neighbours of the source individual (within 200m of the source centre point marker).

To conduct trials, a Bluetooth speaker (UE BOOM 2, Logitech) was placed in the centre of the targeted territory. Markers were placed to provide indicators of distance away from the speaker for the playback observer. Once set-up, the target individual from the territory needed to be identified. This was achieved through the playback of a "chink" call, recorded from an adult in the tested population. The chink call would be played a maximum of 6 times, once every 10 seconds. If the target individual was not identified in the 3 minute period following the last played call, the trial would either be postponed until a subsequent day, or a new target individual was identified.

Once the target individual was identified, the observer instigated the beginning of the playback, a 1 minute period of silence. After this, the first stimuli was broadcast for 2 minutes. After the stimuli ended a period of 2-minute silence occured, before the next stimuli in the second stimuli with observations repeated as per the first playback. This repeated until four periods of active playback were complete.

In this study, approach was the only measure of response utilised, as it has been previously been validated as a measure of territorial response strength in the chaffinch (Leitão & Riebel, 2003; Leitão et al., 2006; Reed, 1982; Slater & Catchpole, 1990). For each 2-minute playback trial, the observer would dictate features of the target individuals behaviour into a voice recorder (iPhone 6s Apple). The approximate ground distance between the subject and the speaker was placed into 5 distance brackets (0-1m, 1-2m, 2-4m, 4-8m, <8m). Distance measures were averaged across 5 second intervals and totalled for the duration of the playback to provide a measure of time spent within each distance bracket.

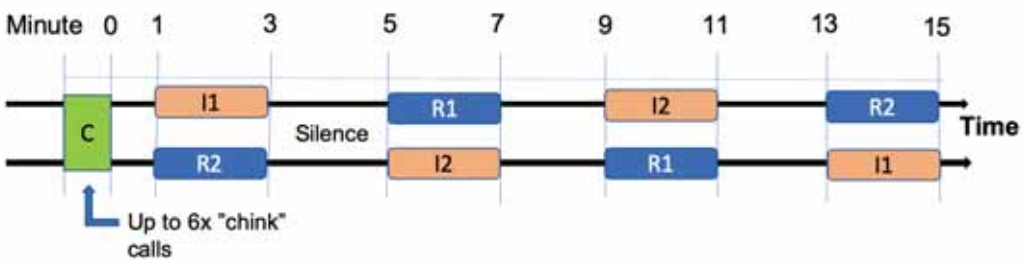


Figure 5.2: Outline of the 15 minute playback procedure. After identifying the location of the bird (possibly through calls), playbacks would alternate between 2 mins of activity (intact stimuli in orange, or recombined in blue) and 2 mins of silence

5.2.4 Data analysis

Firstly, four measures of playback response previously used on chaffinches were calculated (Leitão & Riebel, 2003) for each trial. These were a) the latency for the individual to approach the speaker at the beginning of the trial, the shortest distance the individual approached the speaker during the trial, the time spent within 2m of the speaker, and the time spent between 2-4 metres of the speaker. In addition to this, playback responses were converted into a single score, utilising a method was adapted from protocols developed to investigate playback response in swamp sparrows (Lachlan et al., 2014). To do this, the total time spent by an individual in each distance bracket during each 2-minute playback period was calculated. Then, the time period between the playback stimuli beginning and the latency for the bird to arrive was removed. Time spent in each distance bracket were then converted into a proportion over the total time the bird engaged with a speaker. Next a scaled weighting was applied, whereby the total time spent in each distance bracket was divided by the half-way point between the distance category, such that closer responses would achieve a higher score (Table 5.1). Time spent outside of 8m were not used in score calculation. Finally, we applied a square root manipulation to normalise the score (Sc).

Table 5.1: Weightings for each distance category used to create a response score

Distance category	Division applied
0-1m	0.5
1-2m	1.5
2-4m	3
4-8m	6
>8m	(Scored 0)

Playback response intensity was analysed with a LMM using lme4 in R (Bates, 2007), using a Gaussian family. This resulted in the production of a series of

nested models. where the Sc score was utilised as a response variable. Three series of models were produced for each population, as well as one series combining data from all populations together, including population as a fixed effect. The null model was Response~1 +(1|Type)+(1|Trial), which examined whether the variation in the desired response calculation could be explained by two random factors; type (the song-types used in construction of the playback) and trial (a randomly assigned number for each tested territory).

Nested models of increased complexity were then created by adding fixed effects (Table 5.2, 5.3). These were Phrase Number (the number of phrases in the stimuli song), Order (whether the playback occurred 1st-4th in the series), Stimulus (whether intact or recombined was played) Stimulus Order (whether intact or recombined was played first), and Population. The most appropriate models to explain the variation in responses were selected based upon their AIC scores, as well as the p value reported from a likelihood-ratio test.

Table 5.2: List of nested models incorporating all populations, in tested order.

Model	Description
Null Model	Sc 1 +(1|Type)+(1|Trial)
Model 2	Sc Phrase Number + (1|Type)+(1|Trial)
Model 3	Sc Phrase Number + Order+(1|Type)+(1|Trial)
Model 4	Sc Phrase Number + Order+ Population+(1|Type)+(1|Trial)
Model 5	Sc Phrase Number + Order∗Population+(1|Type)+(1|Trial)
Model 6	Sc Phrase Number + Order∗Population+ Stimulus Order∗Stimuli +(1|Type)+(1|Trial)
Model 7	Sc Phrase Number + Order∗(Population+ Stimulus Order∗Stimuli)+(1|Type)+(1|Trial)
Model 8	Sc Phrase Number + Order∗Population∗Stimulus Order∗Stimuli+(1|Type)+(1|Trial)

Table 5.3: List of nested models in tested order investigated per population

Model	Description
Null Model	Sc 1 +(1|Type)+(1|Trial)
Model 2	Sc Phrase Number + (1|Type)+(1|Trial)
Model 3	Sc Phrase Number + Order+(1|Type)+(1|Trial)
Model 4	Sc Phrase Number + Stimulus+ Stimulus Order+Order+(1|Type)+(1|Trial)
Model 5	Sc Phrase Number + Stimulus x Stimulus Order+Order+(1|Type)+(1|Trial)
Model 6	Sc Phrase Number + Stimulus x Stimulus Order∗Order+(1|Type)+(1|Trial)

5.3 Results

5.3.1 Overall playback response rates

Playback was performed on 16 different individuals in each population (Table 5.4). In the Azores, all 64 trials incurred a response. Of the chaffinches trialled in Catalunya, all but one individual responded to all 4 trials, with the remaining bird absent for a single trial. By contrast in Tenerife, only 9 test subjects responded to each of the 4 presented stimuli. Birds often flew out of the testing area between trials, and sometimes did not return. On other occassions responses to the speaker were restricted to more silent inspection or calling from greater than 8m distance. On 2 occasions, the main aggressor to the playback stimuli was the territorial female whilst the male retained a position further from the speaker, often signalling vocally instead of approaching. Given this high failure rate, it was decided that statistical tests were performed on individuals that responded to all four trials only (The Azores n=16, Catalunya n=15, Tenerife n=8). From here playback findings will be examined first within populations, followed by a comparison of all populations combined.

Table 5.4: Playback experiments performed per population and the number of trials completed

Population	Total	4 Trials	3 Trials	2 Trials	1 Trial	0 Trials
Catalunya	16	15	1			
São Miguel	16	16				
Tenerife	16	8	3	4		1

5.3.2 Playback

5.3.2.1 Catalunya

The model with the lowest AIC score for the Catalunya population, included an interaction between stimulus-type, and stimuli order, but not the two entities separately (Table 5.5). If an intact stimulus was the first played, subsequent trials would incur significantly greater response scores than if a recombined stimulus was played (Mdn score post-intact 0.47, Mdn score post-recombined 0.31, n=45 trials of order number 2-4 24 recombined, 21 intact, Wilcoxon rank sum test, $W = 339$, $p < 0.04$). As greater numbers of recombined stimuli followed a trial beginning with intact stimuli (Figure 5.3), than other intact stimuli, this can minimise the overall effect that stimuli-type itself has (see Table 5.5, model 4). Therefore, whilst there is not direct evidence for the initial prediction of greater responses to precisely learnt songs in continental chaffinch populations, there is

indirect evidence that precisely learnt songs incite greater territorial responses in subsequent playbacks than less precisely learned songs.

Table 5.5: Nested LMM models exploring variation in playback responses in Catalunya

Catalunya Model Description	df	AIC	Log-likelihood	χ^2 test	P($>\chi^2$)
Model 1: Sc 1 +(1|Type) +(1|Trial)	4	-69.45	38.73		
Model 2: Model 1 + Phrase Number	5	-68.31	39.16	0.85	0.35
Model 3: Model 2 + Order	6	-70.23	41.12	3.92	0.04
Model 4: Model 3 + Stimuli + Stimuli Order	8	-70.30	43.19	4.06	0.13
Model 5: Model 4 + Stimuli x Stimuli Order + Order	9	-73.88	45.94	5.58	0.01
Model 6: Model 5 + Stimuli x Stimuli Order x Order	12	-71.73	47.87	3.85	0.28

Model description provides the increase in complexity from top to bottom row, full models are outlines in Table 5.2. Chi-squared (χ^2) tests relate to the previous model in the table. The best supported model (lowest AIC score) is indicated in red. Total sample size was 15 trials.

5.3.2.2 Azores

For the São Miguel population, no model produced a better AIC score than the null model (Table 5.6). Stimuli type, and other fixed effects such as order and stimuli order did not improve the fit of the model (Table 5.6). Compared with Catalunya, the impact of beginning the playback trial with an intact stimulus over a recombined stimulus, was lower; there are no significant differences in the response scores of subsequent trials depending on stimuli order, and if anything, some responses scores for trials following a recombined stimulus are higher than those beginning with intact stimulus (Figure 5.4). Based on the initial hypotheses, these findings indicate the São Miguel population have a relaxed preference to precisely learnt song.

5.3.2.3 Tenerife

In Tenerife, it was similarly found that the null model possessed the highest AIC score (Table 5.7). Therefore, in general there was no effect of stimuli type on the playback scores, and neither was there an effect of stimuli order (Figure 5.5). A model which included a three-way interaction between stimuli order, stimuli and order, did provide a significantly better fit than a model which only included a two-way interaction between Stimuli and Stimuli Order with Order

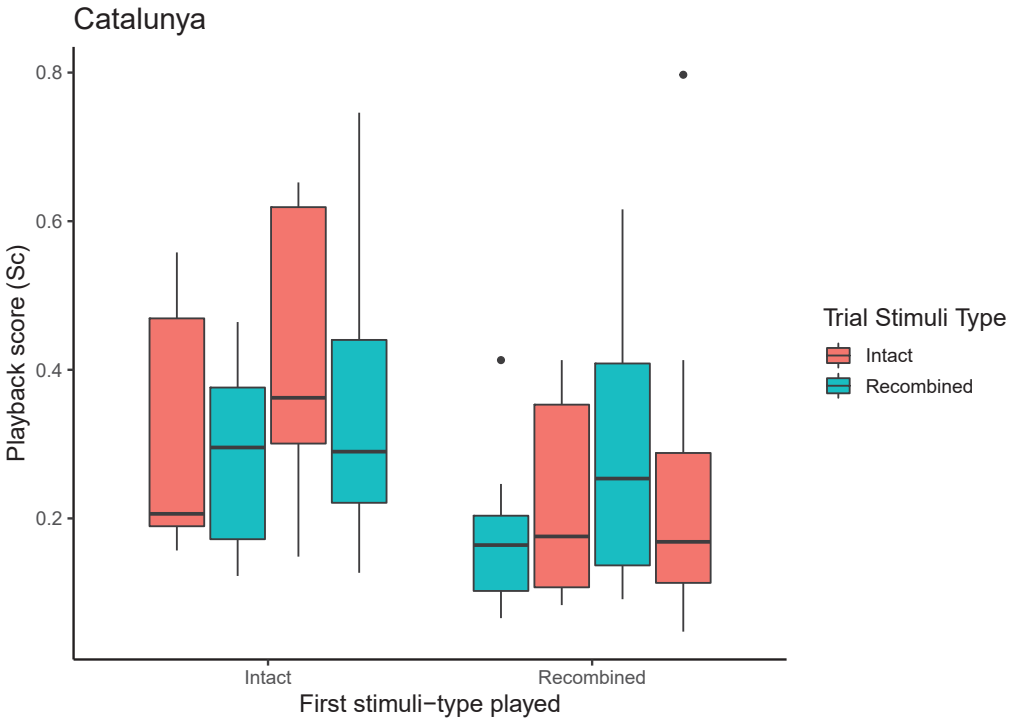


Figure 5.3: The response scores (Sc) for chaffinches responding to intact (red) or recobmined (blue) stimuli in Catalunya. The data is presented in two groups, depending upon whether the first trial presented to a bird was from an intact or recombined stimuli. Each individual was subjected to four successive trials (moving left-right) which alternated between the two stimuli types. Higher response scores are indicative of a stronger response to the playback stimuli.

Table 5.6: Nested LMM models exploring variation in playback responses in São Miguel, Azores

São Miguel Model Description	df	AIC	Log-likelihood	χ^2 test	P($>\chi^2$)
Model 1: Sc 1 +(1|Type) +(1|Trial)	4	-42.18	25.09		
Model 2: Model 1 + Phrase Number	5	-40.18	25.09	0.00	0.99
Model 3: Model 2 + Order	6	-41.13	26.66	3.13	0.07
Model 4: Model 3 + Stimuli + Stimuli Order	8	-37.87	26.94	0.55	0.75
Model 5: Model 4 + Stimuli∗Stimuli Order + Order	9	-36.51	27.26	0.64	0.42
Model 6: Model 5: + Stimuli ∗Stimuli Order∗Order	12	-35.55	29.78	5.03	0.16

Model description provides the increase in complexity from top to bottom row, full models are outlines in Table 5.2. Chi-squared (χ^2) tests relate to the previous model in the table. The best supported model (lowest AIC score) is indicated in red. Total sample size was 16 trials.

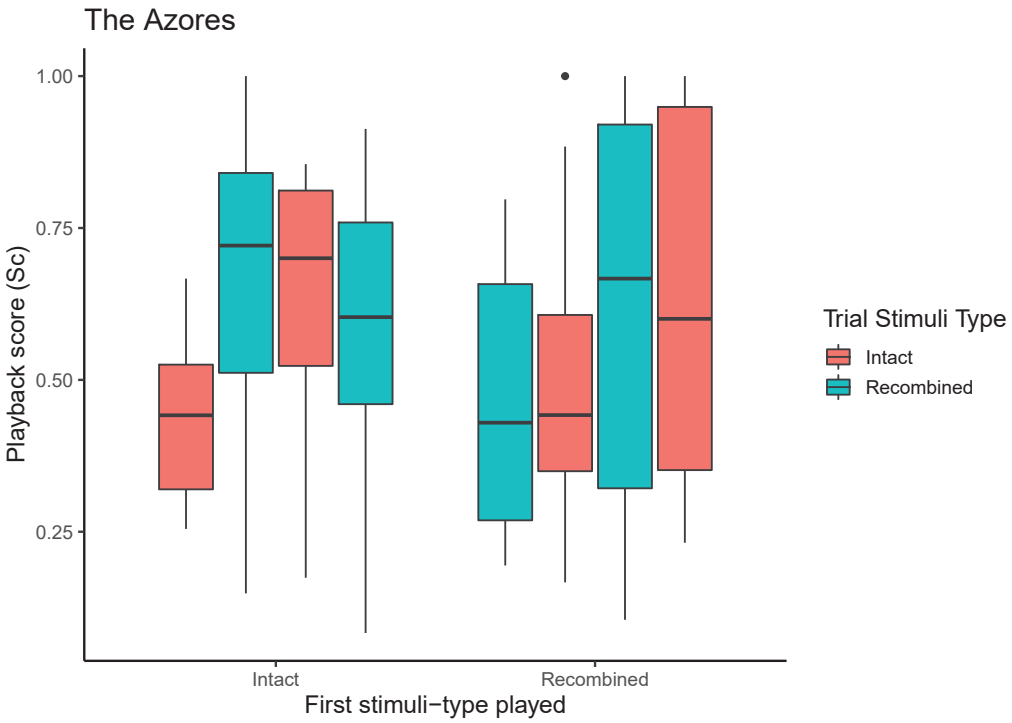


Figure 5.4: The response scores (Sc) for chaffinches responding to intact (red) or recobmined (blue) stimuli in São Miguel, Azores. The data is presented in two groups, depending upon whether the first trial presented to a bird was from an intact or recombined stimuli. Each individual was subjected to four successive trials (moving left-right) which alternated between the two stimuli types.

as an additional effect (Table 5.7). This indicates that the response scores are impacted by timing of the trial relative to others, but this depends on both the stimuli type and the first type of stimuli used. Overall however, based upon the initial hypotheses, the Tenerife population also have relaxed preferences towards precisely learnt songs.

Table 5.7: Nested LMM models exploring variation in playback responses in Tenerife

Tenerife Model Description	df	AIC	Log-likelihood	χ^2 test	P($>\chi^2$)
Model 1: Sc 1 +(1|Type) +(1|Trial)	4	-12.99	10.50		
Model 2: Model 1 + Phrase Number	5	-11.04	10.52	0.04	0.99
Model 3: Model 2 + Order	6	-11.91	11.98	2.88	0.07
Model 4: Model 3 + Stimuli + Stimuli Order	8	-8.10	12.05	0.19	0.75
Model 5: Model 4 + Stimuli∗Stimuli Order + Order	9	-6.56	12.28	0.46	0.50
Model 6: Model 5: + Stimuli ∗Stimuli Order∗Order	12	-9.89	16.95	9.33	0.02

Model description provides the increase in complexity from top to bottom row, full models are outlines in Table 5.2. Chi-squared (χ^2) tests relate to the previous model in the table. The best supported model (lowest AIC score) is indicated in red. Total sample size was 8 trials.

5.3.2.4 Combined

For both of our response measures, the best fitting model included an interaction between playback order and population (Table5.8), and omitted stimuli type. Across all populations, no significant differences were found between stimuli-type and playback response (Figure 5.6). This would suggest that the precision of song learning was not a significant component of chaffinch playback responses. Order effects did significantly affect response rates (Table 5.8), with response intensity increasing following the first trial, particularly in Catalunya and the Azores. Significant increases in responses to playback trials 2-4 following an initial intact stimulus rather than recombined, were not found outside of Catalunya. When considering all trials through the inclusion of stimuli order into the models, no better fit was determined (Table 5.8).

Population-specific playback responses were uncovered , such as individual in São Miguel spending significantly longer less than 2 metres from the speaker than birds from Catalunya (time spent <2m from speaker ± SE, São Miguel 79.60s ± 4.61, Catalunya 44.83 ± 5.96, Wilcoxon rank sum test on 124 playback trials,

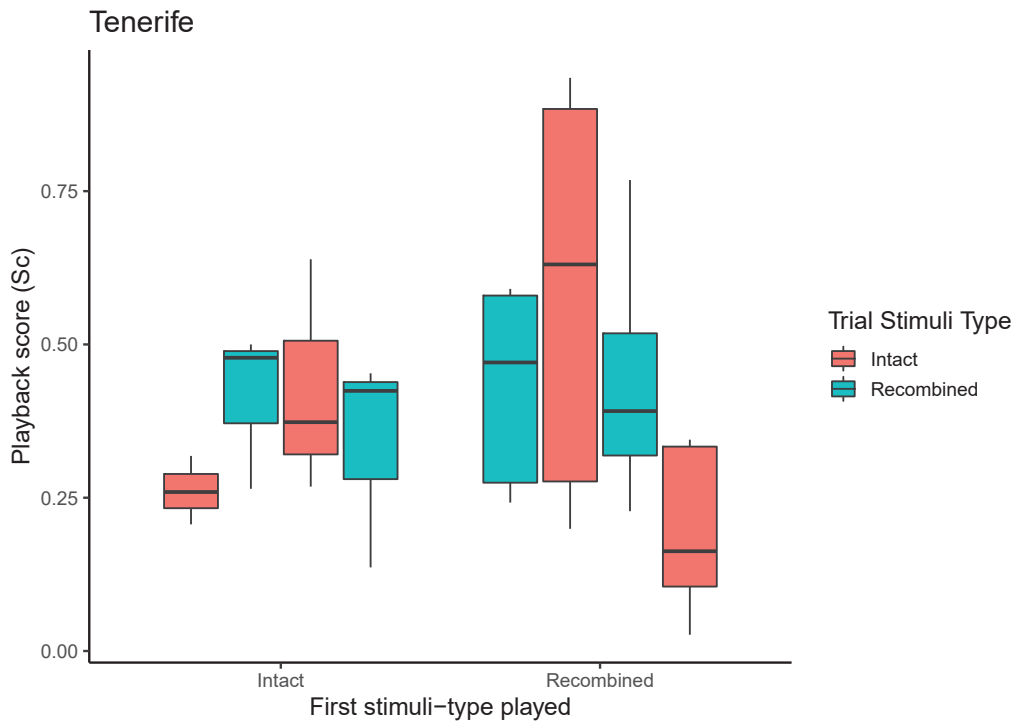


Figure 5.5: The response scores (Sc) for chaffinches responding to intact (red) or recobmined (blue) stimuli in Tenerife. The data is presented in two groups, depending upon whether the first trial presented to a bird was from an intact or recombined stimuli. Each individual was subjected to four successive trials (moving left-right) which alternated between the two stimuli types.

W=980, p<0.001). Such differences were consistent regardless of stimuli-type. When investigating additional factors in the model, the inclusion of population as a 4-way interaction with stimuli-type, order and stimuli order did provide a significantly better fit than one lacking an interaction with population, stimuli and stimuli order (Table 5.8). This finding was consistent with both response metrics and infers potential differences in how populations respond to recombined or intact stimuli, either throughout the trial or if it was the first played. Given that the null models were accepted for the island populations (Table 5.6, 5.7), it seems most likely that this would be driven by the responses of birds in Catalunya.

Table 5.8: Nested LMM models exploring variation in the Sc measure of playback responses between all populations

Response = Model Description	df	AIC	Log-likelihood	χ^2 test	P(>χ^2)
Model 1: Sc 1 +(1|Type) +(1|Trial)	4	544.28	-268.14		
Model 2: Model 1 + Phrase Number	5	545.97	-267.98	0.31	0.57
Model 3: Model 2 + Order	6	546.93	-267.47	1.03	0.30
Model 4: Model 3 + Population	8	544.63	-264.32	6.29	0.04
Model 5: Model 4 + Order x Population	10	543.79	-261.90	4.84	0.08
Model 6: Model 5: + Stimuli + Stimuli Order	13	548.11	-261.05	1.69	0.64
Model 7: Model 6 + Order x Stimuli x Stimuli Order	16	550.83	-259.42	3.27	0.35
Model 8: Model 7 + Order x Population x Stimuli xStimuli Order	28	552.71	-248.36	22.12	0.03

Model description provides the increase in complexity from top to bottom row, full models are outlines in Table 5.2. Chi-squared (χ^2) tests relate to the previous model in the table. The best supported model (lowest AIC score) is indicated in red. Total sample size was 39 trials.

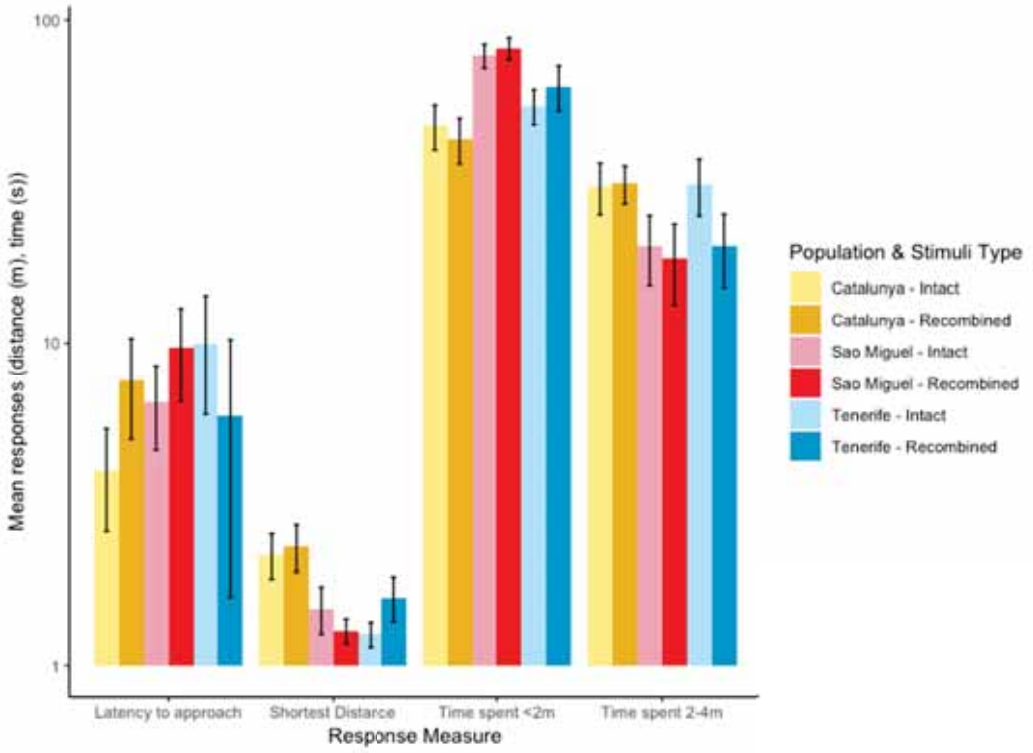


Figure 5.6: Response measurements (mean responses by 8 stimuli pairs +- 1 SE) during the 2 min observation period during playback in 3 chaffinch populations; 1 which exhibit precise song learning (Catalunya - in yellow) and 2 which learn less precisely (São Miguel, The Azores - in red & Tenerife - in blue).

5.3.3 Playback design

5.3.3.1 True Alien vs Familiar

One possibility for the similarity in responses between intact and recombined songs could be that birds may have interpreted both stimuli as being formed from 'recognised' phrases. If birds processed known syllables independently from their sequence, we would expect our recombination stimuli to incur equal responses to the intact song type.

Alternatively, the procedure of the playback - especially the fact that only short gaps were included between stimuli sets - might trigger an attack-all response mechanism, or a response that appears equivalent when measured with our response metrics. Previous playback efforts by Slater and Catchpole (1990) would infer that chaffinches can distinguish between songs from their own population, and more distantly related ones. If this finding was not replicated with my playback design, it would suggest that changes in this design might lead to different results regarding recombination.

To examine this, I conducted a second playback comparing responses by *F.c.moreletti* to same population song types, and to those of *F.c.gengleri*. *F.c.moreletti* was tested as they both demonstrated different precision learning patterns to continental chaffinches, and were the most reliable responders during the original trials. In addition, due to the nature of the Azores being the first colonisation point for the remaining islands, it is likely that effects demonstrated by Azorean birds would be representative of the islands, where birds are harder to test in playback studies.

Utilising the same manipulation procedures for songs as in the previous study, 40 total source songs (2 per song-type, split evenly between populations) were turned into stimuli sets containing song types alternating between the populations. Half of stimuli started with a British song, and half an Azorean to counterbalance the design, as in the original methods. In this experiment, each test subject was presented different song types, to avoid pseudoreplication from using multiple song recordings twice (McGregor et al., 1992). Songs were presented to birds using the same "2 minutes on, 2 minutes rest" procedure as in the first experiment, and responses were compared using the score (Sc) measure. This was chosen as it better discriminates between smaller increments in response distance, which are more profound in Azorean chaffinches, due to their smaller territory size.

Playback responses were again analysed through comparing nested LMM models created using a using lmer in R (Bates, 2007), using a Gaussian family (Table

5.9). The null model was Response Sc~1 +(1|Type)+(1|Trial), which examined whether variation in response scores can be explained by two random factors; type (a randomly assigned number given to the particular song-type used to create the stimuli) and trial number. Fixed effects added to the models include: Phrase Number (the number of phrases in the stimuli song), Order (whether the playback occurred 1st-4th in the series), Stimuli (whether the song is of an Azorean or British origin) Stimuli Order (whether an Azorean or British chaffinch was played first). The most appropriate models to explain the variation in responses were selected based upon their AIC scores, as well as the p value reported from a likelihood-ratio test.

Table 5.9: Nested LMM models exploring variation in playback responses between local and foreign songs in São Miguel, Azores

Model	Description
Null Model	Sc 1 +(1|Type)+(1|Trial)
Model 2	Sc Phrase Number + (1|Type)+(1|Trial)
Model 3	Sc Phrase Number + Order+(1|Type)+(1|Trial)
Model 4	Sc Phrase Number + Stimulus+ Stimulus Order+Order+(1|Type)+(1|Trial)
Model 5	Sc Phrase Number + Stimulus∗Stimulus Order+Order+(1|Type)+(1|Trial)
Model 6	Sc Phrase Number + Stimulus∗Stimulus Order∗Order+(1|Type)+(1|Trial)

5.3.3.2 Results

All 10 tested individuals responded to all 2-minute trials presented. Despite a trend towards Azorean stimuli incuring greater responses, this was not significantly greater than responses to songs of British origin (Figure 5.7). A stronger trend was also evident for greater response scores for individuals which were played an Azorean stimuli first, but again this was not significantly greater than those played British stimuli first (Azorean first score mean 0.69, British score mean 0.50, n=10 pairs, Wilcoxon Ranked-Sum test, W = 118, p=0.07). Of the nested models, the null model was found to provide the best fit for the response scores (Table 5.10). The inclusion of stimuli-type into the models was marginally not significant, with no significant differences found between the playing of an Azores song compared to a British song (Figure 5.7). For the 3rd trial conducted, which would be a repeat of the first stimuli-type, all Azorean stimuli yielded greater responses than the paired British song (Figure 5.7). Though the sample size of a specific trial order was not sufficient enough to result in significant differences, this may indicate an underlying relationship between stimuli origin (Azorean v British) and territorial response. In relation to our hypotheses, this suggests that changes

in experimental design might yield different results in both playback experiments conducted.

Table 5.10: Nested LMM models exploring variation in the Sc measure of playback responses between local and foreign songs presented to *F.c.moreletti*

Azores v British Model Description	df	AIC	Log-likelihood	χ^2 test	P($>\chi^2$)
Model 1: Sc 1 +(1|Type) +(1|Trial)	4	-2.39	5.19		
Model 2: Model 1 + Phrase Number	5	-0.85	5.42	0.45	0.50
. Model 3: Model 2 + Order	6	1.11	5.44	0.03	0.86
Model 4: Model 3 + Stimuli + Stimuli Order	8	0.29	7.85	4.82	0.09
Model 5: Model 4 + Stimuli∗Stimuli Order + Order	9	2.03	7.99	0.26	0.60
Model 6: Model 5: + Stimuli ∗Stimuli Order∗Order	12	3.25	10.38		0.18

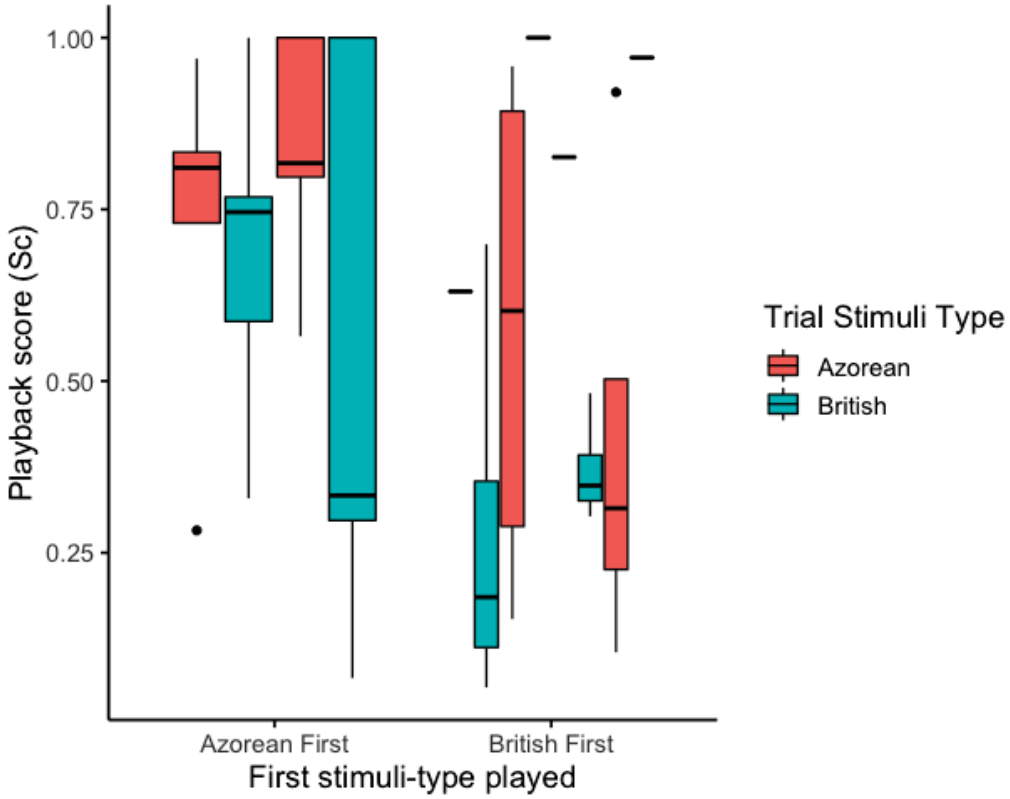


Figure 5.7: The response scores (Sc) for Azorean chaffinches responding either to local Azorean song, or British song. The data is presented in two groups, depending upon whether the first of the four songs presented to an individual was British or Azorean. Stimuli then alternated in successive trials (moving left-right)

5.4 Discussion

We found inconsistent evidence for the hypothesis that chaffinches respond differently to intact and recombined stimuli, if they learnt song less precisely. In Catalunya, where birds learn songs precisely (Lynch & Baker, 1993), there was evidence that the stimuli-type an individual was first exposed to, could affect responses in subsequent playbacks, which is in line with the idea that birds discriminate between intact and recombined songs. There was no evidence of an evolution in preferences towards innovative songs in either of the Atlantic Islands. But when all populations were included one statistical model, no significant interaction was found between population and stimulus type. Our results therefore only provide weak support for the hypothesis that island chaffinches have relaxed preferences for precisely learned songs, and we cannot confidently rule out the hypothesis that preferences have not diverged between island and mainland populations. The lack of discrimination between mainland and local songs in the Azorean population suggests that our experimental design may need refinement, in particular to reduce strong and complex order effects.

It might be the case that chaffinches, do not discriminate against less-precisely learned songs. This would be in contrast to swamp sparrows, where individuals discriminate against poorly-learnt copies of a song-type, compared to more typical versions (Lachlan et al., 2014). It was surmised here that discrimination was likely due to the precision of song functioning as an honest signal of developmental stress, and its resulting impact on male condition (Nowicki, Searcy, & Peters, 2002a; Nowicki et al., 1998). However, if chaffinches do not discriminate in the same manner, no selective pressure would be acting upon a bird that was signalling they had been developmentally stressed. Given that chaffinches on the continent appear to be learning as precisely as possible (Riebel et al., 2015), another mechanism would therefore need to be driving precise song learning. Chaffinches have been found to discriminate against songs with less trill phrases (Leitão et al., 2006; Riebel & Slater, 1998b), whilst males discriminate against songs missing the terminal flourish phrase (Leitão & Riebel, 2003), indicating songs would likely be under some degree of sexual selection. Other proposed drivers for the evolution of precise learning under sexual selection include song-type matching and individual recognition (Brenowitz & Beecher, 2005), and though these appear unlikely for chaffinches (Lachlan & Slater, 2003; Lachlan et al., 2013), they cannot be ruled out without further evidence (Riebel et al., 2015).

In the second study conducted, it was found that islands chaffinches would not discriminate against foreign songs. This would differ from Slater and Catchpole

(1990) who found that chaffinches on Tenerife would discriminate against British songs. This might be indicative of behavioural differences between the Azorean *F.c.moreletti* and Tenerife *F.c.canariensis*. For example, the increased frequency of territorial invasions and lower species diversity on the Azores (Dennison, 1991; Garcia-del Rey, 2011), could render discriminating against the songs of invaders too costly, and instead favour an attack-all invaders behaviour. Alternatively, the smaller territory sizes on the Azores (Dennison, 1991), could mean that the difference between a discrimination and an aggressive response is less determinable, as individuals may remain close to the speaker only to reduce the risk of invading their neighbour's territory.

A more plausible conclusion which can be drawn from both playback studies is that an issue with the experimental design comprimised the findings that could be made. One potential avenue for this to occur would be due to the response metrics utilised. In other songbird playback studies, a variety of other measures aside from distance to the speaker have been incorperated into measuring response strength, including as flights over the speaker, number of songs produced, number of phrases in song responses or other percieved aggressive behaviours (McGregor, 1992; Brindley, 1991; Burt et al., 2001; Kroodsma, 1986; Martin, Fotheringham, Ratcliffe, & Robertson, 1996), including in studies of the chaffinch (Reed, 1982; Riebel & Slater, 1998b). However, as a species, it is generally well recognised that the approach to the speaker is generally the primary initial response a chaffinch has to encountering playback (Leitão & Riebel, 2003; Leitão et al., 2006; Reed, 1982; Slater & Catchpole, 1990). Whilst males can respond in song, generally this occurs after an initial approach. My experience of attempting to use playback to entice chaffinches to sing, reinforced a "less-is-more" philosophy, and to avoid using playback on singing chaffinches, to avoid interrupting them for an extended period. It is therefore more difficult to determine whether the production of songs was an increased or decreased state of aggression, particularly in reference to an already singing bird.

In the original three-population study, observers did additionally record flights over the speaker and songs produced as responses measures, utillsing both in an alternative composite multivariate response measure utilising a Principle components Analysis. Models were produced identically to those above, except using the first principle component as the response, and findings compared. In all four cases, there was no difference when using the principle component approach, with the model scoring lowest in the AIC score remaining the same. As such, it was deemed that only one of the analytical methods needed to be presented, and for simplicity, the principle component approach was the one not included.

The most likely problem with the study design in my opinion, was that responses to a given stimuli-type are likely to have continued to affect those of the opposite stimuli-type in later trials, leading to a reduction in observed differences between the conditions. By finding some indirect evidence of discrimination against less precisely learned song in Catalunya post-initial playback, one could infer that continental chaffinches discriminate against less precisely learnt songs in line with the initial prediction, but this would require a different experimental design to confirm. Order effects may have also compromised evidence for discrimination of less-precisely learnt songs on the Atlantic Islands. But based on the above findings, reduced song learning precision in the Atlantic Islands has occurred in the presence of relaxed preferences or discrimination for precisely learnt songs. What still remains unclear is whether this represents an evolution in behaviour from the source continental population.

Findings by Lachlan et al. (2013), found the degree to which syntactical structure was less evident in chaffinch populations correlated with the number of colonisation events they had experienced. In this study, I found no evidence of differences in song discrimination between island populations, which are believed to have experienced different numbers of colonisation events (Griswold & Baker, 2002). One possibility is that the degree of song evolution might not correlate with tangible differences in song discrimination. Whilst the number of historical colonisation events could have driven reduced precise song learning (Lynch & Baker, 1993) and relaxation in syntactical structure (Lachlan et al., 2013), this may occur with an equal degree of relaxation for song preferences. Alternatively, differences may have been present between how the island populations discriminate precisely learnt songs but were not picked up by the measures of response used in this study. Data collection in Tenerife proved more difficult than either of the other populations. Greater territorial displays by females, regular null responses, frequent neighbour invasions, montane terrain and the presence of another *Fringilla* species all contributed to disrupted data collection and a higher playback failure rate. It may be the case that increased sampling in Tenerife in future, could compensate for this, and might give rise to clearer population differences within the islands.

The experimental design utilised for these experiments was different from what was initially planned, following biases in responses of pilot studies. A two-speaker arrangement was planned to be used, as it has in other song discrimination experiments (Leitão & Riebel, 2003; McArthur et al., 1981; Searcy et al., 1981; Stoddard, Beecher, Horning, & Willis, 1990). In such a set-up, a pair of speakers are placed in a territory, with responses measured upon the bias in approaches

made in one speaker vs another. During pilot trials, instead of approaching speakers based upon the stimuli type, individuals instead display strong side-biases regardless of stimuli-type. These biases were hard to predict, and it was difficult to place the speaker in situations which mitigated them. One option is that this was caused by an individual's previous experience within their territory. Alternatively, the manipulation may have been too subtle for birds to distinguish, when both signals were played together. As a result, a one-speaker designed was favoured.

The benefit of our repeated-measures design was that testing of an individual could be completed within a single day (Martin & Martin, 2001). This differs from other single-speaker, repeated-measure playback experimental designs which recorded the responses of individuals on different days (McArthur et al., 1981; Nowicki, Searcy, Krueger, & Hughes, 2002; Slater & Catchpole, 1990). By testing individuals on different days, factors such as locating the same individual, changes in weather, temperature, time of day, food availability, predator interactions and breeding season timings, may all affect the additional response measures collected (Kroodsma, 1986). These were avoided here through running 4 playbacks in succession, but as a result, strong order effects were encountered. These might have been mitigated with a traditional design which had larger time-gaps in between stimuli presentation. However, a study by Rivera-Gutierrez, Pinxten, and Eens (2015) found that playback trials could still affect individuals, even days after the original trial.

A potential compromise for a future playback experiment would be to use a single speaker and play two playbacks to each individual (Lachlan, pers comm). The first would be a contact call which provides a baseline for the individual's response level. The second would be either an intact or recombined stimulus. Difference between the baseline response and intact or recombined stimuli could then be used to judge discrimination between intact or recombined stimuli. Whilst this would require examining more individuals, it would both mitigate order effects and the day-to-day changes which might impact responses.

Future studies examining the function of precise learning also be approached from a number of different perspectives to male v male playback. For example. here we examined how territory holding birds would respond to invasion, but not how territorial invaders respond to precise or less-precisely learnt song. One path for future studies could be to examine territorial retention in relation to the precision for which an individual's song is reflective of the broader population. A broader issue which would still remain in the proposed experimental design,

is that females may possess different preferences or perceive songs differently to males. If song learning precision is maintained through female song preferences, the assessment of male responses alone is not likely to provide the complete picture of the relationship between the precision of song learning and male quality. Across songbird species, assessment of female preferences is much less common than in males (Searcy, 1992a). Searcy (1992a) placed this discrepancy is placed upon a lack of methodological framework to examine females. In chaffinches' females are usually more reticent to approach playbacks, and though previous studies of preferences have been conducted (Leitão et al., 2006; Riebel & Slater, 1998b), some produced inconclusive results (Riebel & Slater, 1998b). Females examined in these studies were wild-caught, but studied in captivity, and one of the factors behind the inconclusiveness of the results was that chaffinch females struggle to respond naturally in captivity (Riebel & Slater, 1998b). Recently, several operant experiments have been successfully conducted on wild passerines (Cauchoix, Hermer, Chaine, & Morand-Ferron, 2017; Morand-Ferron, Hamblin, Cole, Aplin, & Quinn, 2015; O-Shea, Serrano-Davies, & Quinn, 2017). If such designs could be adapted such that they are effective in comparing song preferences in chaffinches, then females preferences may yet be examined.

5.5 Conclusion

This study investigated whether male chaffinches discriminate against songs which were less precisely learnt, and whether this discrimination had changed in chaffinch populations which learn song less precisely. In general, evidence for discrimination of less precisely learnt songs was inconclusive, with males showing no differences in responses in relation to stimuli type in all populations examined. Indirect evidence of discrimination was found in Catalunya, which was in line with what was initially predicted. Strong order effects were present throughout the study as a result of our chosen experimental design, and through changes proposed here, future studies could mitigate order effects and determine the link between the degree of discrimination against precise song learning, and its maintenance within a population.

Chapter 6

Discussion

6.1 A recap

Identifying differences in how individuals learn is the key to understanding the evolution of cultural behaviour. The songs of songbirds provide a rare case of culturally transmitted behaviour which is learnt with extremely high diversity, yet there is no clear consensus on how different styles of song learning evolve. Though there is typically little within-species variation how individuals learn to sing, isolated populations can vary greatly. Comparison of song learning in related individuals from continental and island populations, could therefore demonstrate ways in which ways song learning can differ, which can in turn be used to highlight the underlying processes which cause this to occur. In this thesis, I tackled this through comparing Atlantic Island and European populations of the chaffinch genus *Fringilla* from 3 perspectives.

1. How does song development evolve?
2. What can cause female song to become present in a species?
3. Does the degree of discrimination of less precisely learnt song reflect the rate of song learning precision?

In answering these questions, I found two, recently evolved differences in the Atlantic Island chaffinches: slower song development and female singing. Previous studies had indicated that island populations showed reduced precision of learning (Lynch & Baker, 1993) and reduced syntactical structure (Lachlan et al., 2013); together with my results a more complete profile of differences between continental and islands Fringilla can now been identified (Table 6.1). In this final chapter,

I aim to evaluate the differences in song learning between the Atlantic Islands and continental chaffinches and use the available evidence to better understand the factors which have resulted in the evolution of song. I then use these links to produce a new framework for how song learning may evolve.

6.2 How is song learning different in the Atlantic Islands *Fringilla*?

By comparing British and Atlantic Islands *Fringilla* in this thesis, I have been able to build a more complete profile of how these populations differ in how they learn song. In the British chaffinch *F.c.gengleri*, only males produce song, which they sing within their breeding territory, held between February-July (Marler, 1956b, 1956a). These chaffinches typically learn a song repertoire of 2-3 songs, which are precise copies of the phrases and phrase transitions heard from other males (Lachlan & Slater, 2003; Riebel & Slater, 1999b). Yearlings start to signal territory ownership through the production of subsong, usually between day of the year 55-70. Subsongs have high phrase diversity, low phrase redundancy and low rhythmic consistency (Chapter 2).

After several days of producing subsong, *F.c.gengleri* yearlings make gradual changes to the songs they produce, decreasing the diversity of phrases and increasing the consistency with which they sequence phrases (measured through calculating phrase redundancy). Rhythmic consistency also increases during this time. *F.c.gengleri* learn all of their songs over a period of 30-45 days, though do not appear to learn them all at the same rate. It is not clear whether this is a consequence of statistical processes in learning during sensorimotor feedback, or whether this an adaptation to prioritise learning more effective songs. Developing *F.c.gengleri* only seem to produce imitations of chaffinch songs that they keep in their adult repertoire, though some memorised heterospecific song may be removed through a process of selective attrition. By day of the year 90-100, yearling singing is similar to that of adults; songs are of low phrase diversity, high redundancy and high rhythmic consistency.

As found in Chapter 3, *F.c.canariensis* males on Tenerife also begin development through the production of subsong which has high phrase diversity, low phrase sequential structure and low rhythmic consistency. Compared to *F.c.gengleri*, *F.c.canariensis* appear to be more variable in when they started producing subsong, with some individuals detected producing subsong after year-day 90. Rhythmic consistency did increase over time in *F.c.canariensis* similarly to *F.c.gengleri*. But

Table 6.1: An extension to the summary of study populations presented in Chapter 3, with findings from this thesis added in blue, alongside the chapter this was examined.

Scientific Name	*F.c.gengleri*	*F.c.canariensis*	*F.teydea*	Previous Studies / Thesis Chapter
Colonisation				
Locations studied	Great Britian / Catalunya	Tenerife	Tenerife	
Natal Population	Pleistocene refuga	North Atlantic Isles	Northern Africa	(Griswold & Baker, 2002)
Colonisation date est.	<30,000 ya	c. 400,000 ya	c. 2,000,000ya	(Griswold & Baker, 2002; Marshall & Baker, 1999; Sangster et al., 2016)
Ecology				
Breeding habitat	Temperate mixed	Laurel forest	Pine forest	(Slater & Catchpole, 1990)
Seasonality	High	Low	Low	(Fernández-Palacios et al., 2011)
Predation risk	High	Low	Low	(Garcia-del Rey, 2011)
Heterospecific competition	High	Low	Low	(Garcia-del Rey, 2011; Lachlan et al., 2013)
Territorial behaviour	February - July	All year	Unknown	5

Table 6.1: Continued.

Scientific Name	*F.c.gengleri*	*F.c.canariensis*	*F.teydea*	Previous Studies / Thesis Chapter
Morphology				
Beak size	Similar across Europe & North Africa	Larger than *F.c.gengleri* & *F.c.coelebs*	Larger than *F.c.canariensis*	(Grant, 1979)
Body weight	Similar across Europe & North Africa	Larger than *F.c.gengleri* & *F.c.coelebs*	Larger than *F.c.canariensis*	(Grant, 1979)
Adult mantle colouration	Brown	Blue	Blue-grey	(Collar et al., 2010; García-Del-Rey & Gosler, 2005)
Yearling mantle colouration	Brown (as adult)	Green-brown	Grey-brown	(Collar et al., 2010; García-Del-Rey & Gosler, 2005)
Song				
What is learned				
Typical song repertoire size	2-4	Anywhere from 1-6+	1, occasionally 2	(Lifjeld et al. (2016); Lynch and Baker (1993); Slater et al. (1980); Lachlan, in prep)
Precision learning of song-types	Yes	No	Yes	(Lachlan, in prep)
Sequential structure learning	High	Low	Likely High	(Lachlan et al., 2013)
Neighbour song sharing	Low	High where present	High	(Lachlan, in prep)
Female song present	None	Yes	Yes, and in a duet	4

Table 6.1: Continued.

Scientific Name	*F.c.gengleri*	*F.c.canariensis*	*F.teydea*	Previous Studies / Thesis Chapter
Male Song Development				
Phrase structure & sequencing change	Gradual changes towards memorised song	Gradual changes towards memorised song	Unknown	2
Sensorimotor development rate	Regular	Slow	Slow	2,3
Rhythmic development	Yes	Yes	No	2,3
Phrases learnt in correct sequential position	Sometimes	N/A	Unknown (likely yes)	2
Heterogenous song learning	Present, individual variation	Unknown	Unknown	2
Overproduction	Little evidence	Unknown	Little evidence	2,3
Territorial Behaviour				
Discrimination against less precisely learnt song	Indirect evidence	No evidence	No evidence	5

song development, in terms of increases in the stereotypy of sequences, changes at a considerably slower rate than would be found in *F.c.gengleri*. The peak rate of development in song redundancy happens significantly later in the year, and unlike in *F.c.gengleri*, may have further spells of song development occuring after their first Spring. Much of the development of song occurs after having paired with a female, whereas in *F.c.gengleri*, phrase sequential structure is high when yearlings start to pair up. *F.c.canariensis* females also produce songs themselves (Chapter 4), which are produced more rarely than male song, and are very different in structure. It remains unknown when female songs are acquired and how they develop, and though they seem likely to aid territorial defence, may also possess other functions. Females possess one song-type, though this can be quite variable, whilst fully developed male *F.c.canariensis* possess anywhere from 1-8 song-types (Lachlan, in prep).

F.teydea male yearlings began defending territories with songs which show markedly higher sequence redundancy than those of *F.coelebs* yearlings at a similar time-point, though lower than found in *Fringilla* adults (Chapter 3). In the comparable time period for which *F.c.gengleri* undergo their entire sensorimotor development, *F.teydea* yearlings make no significant changes in their levels of phrase diversity, redundancy, or rhythmic consistency. With adults also likely to be high in their levels of redundancy (Chapter 3), this indicates that *F.teydea* also develop slowly like *F.c.canariensis*. Another similarity between these two populations is that the females sing (Chapter 4). In the case of *F.teydea*, females sing in a loosely-timed duet with the ending of the male song. Finally, although neighbour song sharing is high in *F.teydea* (Lachlan, in prep) and individuals usually only possess a repertoire of one song type, no evidence of overproduction was found.

In the literature, song development is largely regarded as a process that occurs in stages; chiefly subsong, plastic song and crystallisation (Nottebohm, 1970; Clark et al., 1987). Yet when looking at the developmental trajectories for phrase diversity, sequential structure, and rhythm, where these measures increase, they did so gradually. Other than referring to the beginning of development as subsong, and the end as crystallised song, it was difficult to define when the birds were in a discrete song development stage. Adding to this, I found clear evidence of heterogenous song learning, when birds could be considered producing crystallised song for one song-type, whilst still being variable in another. If supported by similar findings in further studies of song development, it might be worth considering whether a more continuous model of vocal learning can instead be supported.

6.3 Why has song evolved?

The relationship between the evolution of song and the underlying factors which cause this to occur remain unclear (Catchpole & Slater, 2008; Slabbekoorn & Smith, 2002a). Through previous studies and now through this thesis, a more complete profile of differences in song learning in related *Fringilla* populations has been attained. Such improvements can therefore be used to determine the underlying factors which are more likely to be responsible for evolutionary changes in patterns of song learning.

Underlying factors previously identified as being potentially responsible for changes in song learning in isolated populations include inter-related ecological changes, such as reduced seasonality or finite breeding territories on islands (Covas, 2011; Losos & Ricklefs, 2009; Whittaker & Fernández-Palacios, 2007). Interspecies dynamics may also be different on islands, where there is expected to be less predation, parasitism and heterospecific competition, and the potential for higher population densities (MacArthur et al., 1972; Whittaker & Fernández-Palacios, 2007). Alternatively the process of arriving into isolation, such as through founder effects of island colonisation may have continued to have long lasting impacts on song (A. J. Baker & Jenkins, 1987; Potvin & Clegg, 2015; Thielcke, 1973). This may either be due to a weakening of sexual selection, or through gene-culture coevolutionary processes relating to colonisation (Griffith et al., 1999; Lachlan & Slater, 1999).

In a study of change in syntactical structure in *F.coelebs* in the Atlantic Islands, Lachlan et al. (2013) linked their findings to colonisation, on the basis that the pattern of change in syntactical structure mirrored the pattern of colonisation events (Suárez et al., 2009). Two of the most likely mechanisms for this proposed in Lachlan et al. (2013), relate to relaxation in biases for song learning, under situations of high cultural drift. This might also provide an explanation for why *F.teydea* learn songs differently to Atlantic Islands *F.coelebs*, as under conditions of high drift, different outcomes may result from the same founder population (Podos, Huber, & Taft, 2004).

One hypothesis through which a relaxation in song learning biases could result in slower development is weaker sexual selection. In Chapter 5, it was uncovered that whilst chaffinches most likely discriminate against songs which are learnt less precisely on the continent, in the Atlantic Islands there is little evidence of any discrimination. This would indicate a relaxation in the underlying selection pressure for developing songs which are learnt precisely, a trait which would

likely incur a high energetic cost (Marler et al., 1988). If learning songs precisely became less of a priority for an Atlantic Islands male, it might be expected they would put lower physiological investment into its development, which may result in the process taking longer. Based upon findings in Chapter 3, the learning of high sequential structure in the Atlantic Islands *Fringilla* would likely occur between their first and second breeding season. One key piece of evidence that remains outstanding for this hypothesis, is whether male responses to precisely learnt songs, also reflect song preferences in females. Female preferences are typically less commonly examined than males due to a lack of methodological framework (Searcy, 1992a), but adaptations on recent operant experiments on wild passerines (Cauchoix et al., 2017; Morand-Ferron et al., 2015; O-Shea et al., 2017) may provide a basis through which female preferences could be examined in chaffinches.

In the case of female song, as discussed in Chapter 4, it is unlikely to have arisen from a cultural bottleneck. Furthermore, based on the findings in Chapter 5, where I reported no difference in discrimination of precise and less-precisely learnt songs, it is unlikely that female song compensates for any reduced function of male song, due to how precisely it is learnt. One hypothesis which can be readily considered for female singing would be due to broader ecological differences between the mainland and the Macaronesian islands. Female song has already been correlated with tropical environments with low seasonality (Odom et al., 2014; Slater & Mann, 2004), such as those found in the Canary Islands where the majority of female song recordings were made. These are likely to be the causal factors behind the year-round territory ownership found in Chapter 4. Increases in the length of territorial ownership as well as potentially increased territorial interactions (Dennison, 1991), would likely increase investment in behaviours utilised to defend territories. One of these, could be female song.

Sensorimotor phase onset is linked to seasonal fluctuations in hormone production (Marler et al., 1988; Nottebohm et al., 1987). The reduction in seasonality found in islands (Weigelt, Jetz, & Kreft, 2013) may correspond to changes in hormone production, which could also delay or prolong sensorimotor development. Similarly, increases in androgen have already been found to result in female singing in continental chaffinches, though songs produced be injected females resembled male song in structure (Kling & Stevenson-Hinde, 1977).

Another consideration to be made when considering environmental impacts on song development in the chaffinches, is that whilst some changes have been observed across the Atlantic Islands, slow learning has currently only been investigated on

Tenerife. Therefore, it could also be the case that slow learning is a particular response to conditions of this island. One might propose that this could be due to interactions between the two *Fringilla* species, for which Tenerife uniquely hosts among the Atlantic Islands (Carrascal et al., 1992; Garcia-del Rey & Cresswell, 2005), though this is not across the entirety of their range. However, the yearling individuals assessed in Chapter 3 were largely from allopatric populations of these species, except for 2 *F.c.canariensis* yearlings.

One aspect of female song which is different to the changes in Atlantic Islands song reported by Lynch and Baker (1993) and Lachlan et al. (2013) is that this may be present in other peripheral chaffinch populations but be unreported due to its rarity. Chaffinches in North Africa for example, are relatively understudied compared with continental and British birds. This population experiences a number of environmental conditions similar to those of the Atlantic Islands chaffinches, such as low latitude (Perktaş et al., 2017) and heterospecific competition (Lynch & Baker, 1993), but live as part of the continental population. In addition, song learning is also found to be more variable than continental populations (Lynch & Baker, 1993), suggesting that some changes in song learning may have occurred in this population too.

6.3.1 Conclusions

When bringing these all together, the main hypotheses of factors which have resulted in song learning changes uncovered in this thesis, add to those suggested in Lachlan et al. (2013). Relaxation in sexual selection may have led to slower sensorimotor development, whereas the reduced seasonality may have promoted year-round territoriality, and in turn female singing. Alternatively, seasonality might impact on hormonal production in ways which have contributed either to the regular production of female singing or slower learning. In the case of slow learning, it is not yet known whether this trait is exclusive to Tenerife, whilst female singing may also be present in peripheral continental populations. Future studies could add clarity to these hypotheses from a number of approaches. Development in techniques to better assess female song preferences in chaffinches would aid determining whether sexual selection for songs learnt quickly and precisely is more relaxed on the islands. Hormonal sampling of *Fringilla* populations by comparing sexes and continental and island populations would help determine if there is a relationship between prolonged sensorimotor development, and a reduction or lengthening of increased androgen levels. In addition, it would help determine the degree of androgen levels present in singing and non-singing females, and whether these fluctuations also coincide with the development of this behaviour.

Alternatively, examination of the presence of female song and/or slow learning in African chaffinch subspecies, could help separate the respective role of island ecology, or of particular ecological traits found on these islands, in the evolution of these behaviours.

6.4 Self-song memory, slower development and the evolution of song

When comparing how precisely different song components are learnt by chaffinches, the phonology of syllables are copied with similar precision in both Atlantic Island and European populations (Lachlan et al., 2013; Lynch & Baker, 1994). However, island birds sequence phrases they share with individuals around them, in an order unique to themselves (Lynch & Baker, 1993). As found in Chapter 3, Tenerife chaffinches develop their songs more slowly than continental chaffinches. Are these two differences in song learning linked? By examining this possibility, a framework for a developmental model has been designed which might provide an explanation (Lachlan and Cooper, in prep.).

This framework is based upon the statistical learning of phrase transitions, and is represented by two node-networks, in each of which nodes represent memorised phrase-types, and vertices the sequential order of phrases (Figure 6.1c). The thickness of the vertices equate to the probability of that particular phrase transition, such that once songs have crystallised, a small number of transitions will have a maximum vertices strength, and all other transitions will have minimal or no connection. One of the two networks correspond to song perceptual memory (n1), while the other corresponds to song production memory (n2).

In the framework, every time a bird produces a song, its sequence is determined by the probabilities in the song production network, n2. The transitions between the phrases it produces are then checked against those in its memory (Figure 6.1a). This leads to two learning processes. First, if a produced transition matches the perceptual memory, n1, feedback between the networks reinforces the strength of that transition in the production network, n2. This aspect of learning matches the well-established finding that in order for birds to learn how to produce a song, they must be able to hear the songs they produce (Nottebohm, 1968). Second, all produced transitions also reinforce the corresponding transition in the perceptual memory ("the bird remembers what it has produced").

Prior to the start of the sensory-motor phase of development, all phrase transitions

in the production network are equally likely (Figure 6.1c), and sequences are very variable. The process of sequence sampling and reinforcement is then repeated each time the bird sings, which would be thousands of songs over the sensorimotor development of a chaffinch (Figure 6.1d). Song development stops once the perceptual and production networks match each other.

The key parameters of the model, m1 and m2, describe the plasticity of the two networks, i.e., how much they adapt after a song is produced. m1 represents the plasticity of the perceptual network, and m2 that of the production network. The process of development after a particular number of song renditions, is shown in two examples in Figure 6.1d. If m1 is much smaller than m2, then we expect the production network develop as shown in Figure 6.1d, i-iv. The individual begins development producing a wide diversity of phrase transitions, and very quickly would encounter one which matched those memorised from songs of other individuals (Figure 6.1d, i). Each time this occurs, the weighting of that transition increases (Figure 6.1d, ii), until after a number of songs are produced, the individual can reliably produce identical transitions to the model (Figure 6.1d, iii). Because m1 is small, during this process, the perceptual memory does not change during development based on the bird's own production. Figure 6.1d, v-viii details an example of phrase transition change during the development of an individual where m2 is larger, relative to m1. In this case, the perceptual memory adapts to the random sequences of phrases produced earlier in development. Thus, the individual spends longer randomly matching phrases in the network (Figure 6.1d, v), until by chance it begins to produce a particular phrase transition more often than expected. This will update the network resulting in songs formed of these particular transitions (Figure 6.1d, vi-viii), and eventually the repertoire will crystallize. But the transitions learned are likely not to match those memorized before production started.

One potential mechanism which might cause birds to modify their perceptual memories more during song development, is a change in the timing of the sensorimotor phases. Chaffinches possess two sensitive phases when they can memorise song, one just after fledging, and another before sensorimotor development, the following Spring (Nottebohm, 1968; Thielcke & Krome, 1991). In British and European chaffinches, it is thought that the sensorimotor phase, follows this second sensory phase, Figure 6.2). If Atlantic Islands chaffinch sensory or sensorimotor phases have moved such that they overlap to a greater extent, individuals might become more sensitive to songs they produce (Figure 6.2). This could be confirmed in future studies, through depriving captive individuals of songs at various time points, comparable to those performed previously by (Nottebohm, 1968; Thielcke

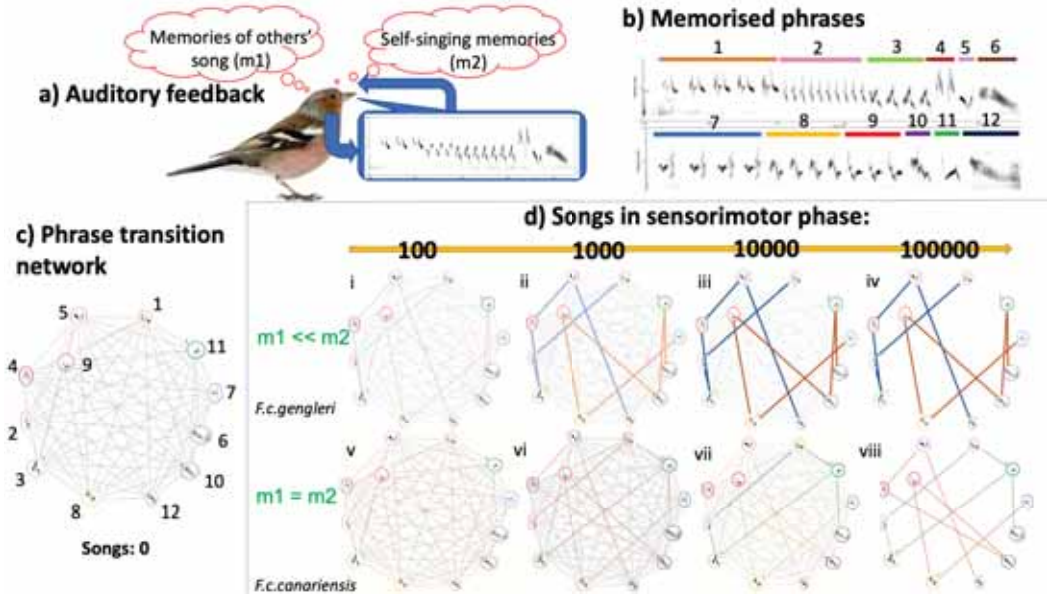


Figure 6.1: Outline of a possible framework for how song learning may change based upon variance in the type of memory to guide auditory feedback. a) A chaffinch produces a song and compares its similarity to its perceptual memories of song as well as song production memory b) Two example songs which have been memorised from other males, with each phrase-type labelled c) A representation of song production memory network (n2) prior to the sensorimotor phase, where phrases and all transitions between each pair of phrases are equal in strength d) Song production memory networks from four stages in development, with two example pathways depending on which song memories (m1,m2) are more utilised in giving sensorimotor feedback. In pathway i-iv m1 has a greater influence than m2, and in pathway v-viii, m2 has a greater influence than m1. Networks are ordered in the number of songs produced over sensorimotor development. Different song-types are represented by different vertices colours

& Krome, 1991).

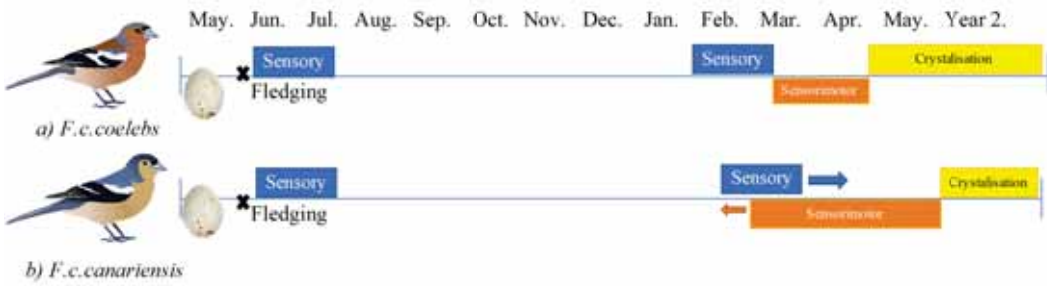


Figure 6.2: Comparison of timings in the key stages of vocal development in chaffinches. A) represents possible timings reflective of development in continental and Britsh chaffinches, and b) includes possible overlap of key phases which may occur in the Atlantic Island chaffinches

In summary, through the empirical findings of how song learning has changed in the islands chaffinches, a prototype of a developmental model has been produced. Through the modification of a single trait, the degree to which an individual utilises memories of their own song production in guiding auditory feedback during song development, the model can predict different learning outcomes similar to those observed in nature. Future work should focus on validating assumptions of the model, as well as exploring whether similar results can be found in other species.

6.5 Future uses for song development in the wild

The methods outlined in Chapter 2 and Chapter 3, highlight how development could be analysed and compared between populations to provide further insight into the process of song learning. As a result of progress made in this thesis, there are further outstanding questions in song development for which these techniques could be applied. One way this could be achieved is through extending comparisons to more closely related taxa. The case for further study of the African subspecies of chaffinch has already be outlined, but these techniques could be used for a broader range of species to investigate other questions regarding song learning traits not found in chaffinches. For example, do open-ended learners develop song differently to closed-ended learners, but lack a period of crystallisation? In dialect learning species, how does the development of a dialect specific song-type differ to that of other memorised songs? A developmental analysis conducted in parallel with controlled song-learning design such as in Mennill et al. (2018) could provide a powerful approach to examine song development experimentally.

One area which could benefit from examining song development using the methods outlined in this thesis, would be the development of song in female songbirds (Riebel, 2016). In some species female singing is different to males (Baptista et al., 1993; Hall, 2009; Hausberger & Black, 1991; Riebel, 2003), but as yet no study has compared how the sexes develop differently (Riebel, 2016). Roper et al. (2018) made inroads into this by comparing songs of males and females during song development, and how these songs compared to adults. However, they did not examine the process of song development in detail. By replicating the techniques outlined in this thesis, questions related to sex-specific learning could be examined. For example, in a species where the males learn differently to females, are these differences a result of a change that occurs during development, or do they possess entirely different patterns of song learning.

If future studies did look to replicate methods utilised in Chapter 2 and Chapter 3 to examine vocal development in the wild, then the target species should possess a number of key characteristics so that data collection is possible. Individuals of the species need to be territorial prior to possession of fully developed song, as this assists in data collection on multiple fronts. For the chaffinches, this meant they could be reliably located during the morning hours. Without this, there would be little chance of re-locating the same individual. In addition, they defended their territories through counter-singing, and would do so to songs produced by speaker playback from adjacent territories. Whilst territoriality in yearling chaffinches was not such that they could be easily captured in mist nets like adults, it would be advantageous if they were, as it would allow for colour ringing to provide another visual identification aid. It should be noted that it is often difficult to detect colour rings when re-encountering birds, and given that data collection often occurs at dawn, visibility can be low. As such, a level of individuality in singing would also aid identification through bioacoustics methods found in Chapter 2.

It would also be advantageous if song development could be captured in 10-15 minutes of solid recording. In the chaffinches, this would usually equate to between 50-100 songs, though this number would be species dependant, and based upon factors such as repetoire size and song complexity. The longer that is required to detect and record birds, the more likely it is that recording sessions can be disrupted or require excessive use of playback which may have prolonged consequences on how that bird responds in future.

Of the three populations measured in Chapter 2 and Chapter 3, *F.c.canariensis* were the hardest to collect data. Habitat-wise, they live in montane laurel forests in Tenerife, though do occupy residential gardens in the wetter North-Western

half of the island. The forests were difficult to navigate due to the density of foliage and their montane terrain. This made it difficult to follow particular individuals when they moved, or approach singing individuals that were down inaccessible cliffs. In addition, the laurel forests are characterised by high rates of rainfall. In the rain, chaffinches are less likely to sing, song recordings are affected by rainfall noise, and recording equipment is susceptible to water damage. In addition to this, responses by a territorial individual were fairly unreliable, with some individuals only singing during the dawn chorus. This made it difficult to record multiple birds on the same day, affecting sampling. To compensate, responses of individuals were observed later in the morning, and those which more reliably responded to playback, were saved for late morning recording sessions. Also, if yearling individuals are readily detectable, then one can be more selective over which individuals they choose to pursue.

F.teydea provided the simplest data collection, despite displaying the least vocal development of the three species analysed in this thesis. The montane pine forests where they reside are sparser than the laurel forests, far more navigable, and less steep, allowing for a recorder to quickly respond if a target individual were to move. The forests are usually above cloud level, and therefore climate conditions were fairly consistent. As a species, the individuals are much tamer than *F.coelebs*, and can be recorded from a few metres away without alarm. Recording collection did remain difficult at times, particularly during periods of mate guarding behaviour, when males pursue territorial females to minimise risk of extra-pair copulations (Hanski & Laurila, 1993; Sheldon & Burke, 1994). However, this behaviour was present in all of our populations, and was responsible for spells of low recording capture, particularly in *F.c.canariensis*. Species which learn songs prior to mate guarding, or other behaviours which reduce their song output would therefore also improve their chance of being a development study species. It could be argued that understanding the timing of development is another highly important factor behind future study species choice. In the species analysed in this thesis, the beginning of song development was only well understood in *F.c.gengleri*. Song development in the Canarian chaffinches were examined at similar dates to those of *F.c.gengleri*. It might be the case that they began developing song earlier. In the case of *F.teydea* though, song detection of all birds (including adults) was low between 17/02/2018 and 28/02/2018.

In summary, new methods for examining development have been documented in this thesis and could be utilised in future to provide further insights into the nature of vocal learning and song evolution. In this thesis, I examined chaffinch genus *Fringilla*, as they possess a number of characteristics which made them suitable

candidates for examining development in this way. If future studies were to replicate these methods on different species, based upon my field experience, they should look to prioritise species possessing a particular set of traits. Individuals should be highly territorial and live in territories which rarely change. They should also sing regularly, and in response to a territorial threat. Finally, it would be recommended that they are sampled in predominantly dry and easy to navigate habitat.

6.6 Closing Remarks

In summary, though songbird species usually conform in how they learn song, there is widespread evidence that on islands, populations can learn songs differently, though there is little understanding of what causes song learning to evolve (Catchpole & Slater, 2008; Slabbekoorn & Smith, 2002a). Previous attempts to examine song evolution in this way have mainly focussed upon what continental and island populations learn (Arcese et al., 1988; Hamao & Ueda, 2000; Morinay et al., 2013; Lachlan et al., 2013; Lynch & Baker, 1993). In this thesis, I instead examined how populations in the chaffinch genus *Fringilla* differ in how males develop songs, how females sing and whether precise learning is linked to discrimination against less precisely-learnt songs. In doing so, I aimed to build a more complete profile of how island chaffinches differ to continental birds which I could then use to clarify factors which have resulted in the evolution of song. I revealed two previously unknown differences within the song learning of the Atlantic Islands *Fringilla*, the presence of female song and slower development, and that it is likely that Atlantic Islands *Fringilla* discriminate less against precisely-learnt song than birds on the continent. Together, these findings led to the development of a new potential mechanism for how song learning may evolve; the degree to which individuals utilise memories of songs they produce to guide auditory feedback during vocal development. These findings point towards relaxation of sexual selection and an increased timespan of territorial ownership in less seasonal conditions, as being likely to have influenced the evolution of song, alonsigde factors presented by Lachlan et al. (2013). However, changes in hormonal productioncannot be ruled out as a cause of either slow learning or female song. Future studies concerning the evolution of song, should look to replicate these methods in the African subspecies, to provide further clarity on how island environments contribute to song learning change. In addition, methods used to analyse song development could be readily be adapted to investigate currently unknown aspects of the song learning process; such as female song development and the differences between open and closed-ended learners.

References

Akçay, C., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1756), 20122517.

Anderson, R. C., Peters, S., & Nowicki, S. (2014). Effects of early auditory experience on the development of local song preference in female swamp sparrows. *Behavioral ecology and sociobiology*, *68*(3), 437-447. doi: 10.1007/s00265-013-1658-7

Arcese, P. (1987). Age, intrusion pressure and defence against floaters by territorial male song sparrows. *Animal Behaviour*, *35*(3), 773-784. doi: 10.1016/S0003-3472(87)80114-8

Arcese, P., Stoddard, P. K., & Hiebert, S. M. (1988). The form and function of song in female song sparrows. *Condor*, 44-50. doi: 10.2307/1368431

Arnold, A. P. (1992). Developmental plasticity in neural circuits controlling birdsong: sexual differentiation and the neural basis of learning. *Journal of Neurobiology*, *23*(10), 1506-1528. doi: 10.1002/neu.480231010

Aronov, D., Veit, L., Goldberg, J. H., & Fee, M. S. (2011). Two distinct modes of forebrain circuit dynamics underlie temporal patterning in the vocalizations of young songbirds. *The Journal of Neuroscience*, *31*(45), 16353-16368. doi: 10.1523/JNEUROSCI.3009-11.2011

Baker, A. J., Dennison, M. D., Lynch, A., & Le Grand, G. (1990). Genetic divergence in peripherally isolated populations of chaffinches in the atlantic islands. *Evolution*, *44*(4), 981-999. doi: 10.2307/2409560

Baker, A. J., & Jenkins, P. F. (1987). Founder effect and cultural evolution of songs in an isolated population of chaffinches, (*Fringilla coelebs*), in the chatham islands. *Animal Behaviour*, *35*(6), 1793-1803. doi: 10.1016/S0003-3472(87)80072-6

Baker, M. C. (1994). Loss of function in territorial song: comparison of island and mainland populations of the singing honeyeater (*Meliphaga virescens*). *The Auk*, *111*(1), 178-184. doi: 10.2307/4088516

Baker, M. C. (2006). Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection on songs. *Ethology*, *112*(8), 757-771. doi: 10.1111/j.1439-0310.2006.01212.x

Baker, M. C., Baker, M. S., & Baker, E. M. (2003). Rapid evolution of a novel song and an increase in repertoire size in an island population of an australian songbird. *Ibis*, *145*(3), 465-471. doi: 10.1046/j.1474-919X.2003.00190.x

Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, *15*(1), 163-168. doi: 10.1093/beheco/arg090

Baptista, L. F. (1974). The effects of songs of wintering white-crowned sparrows on song development in sedentary populations of the species. *Zeitschrift für Tierpsychologie*. doi: 10.1111/j.1439-0310.1974.tb01794.x

Baptista, L. F. (1977). Geographic variation in song and dialects of the puget sound white-crowned sparrow. *The Condor*, *79*(3), 356-370. doi: 10.2307/1368014

Baptista, L. F. (1985). The functional significance of song sharing in the white-crowned sparrow. *Canadian journal of zoology*, *63*(8), 1741-1752. doi: 10.1139/z85-263

Baptista, L. F., & Morton, M. L. (1988). Song learning in montane white-crowned sparrows: from whom and when. *Animal Behaviour*, *36*(6), 1753-1764.

Baptista, L. F., & Petrinovich, L. (1986). Song development in the white-crowned sparrow: social factors and sex differences. *Animal Behaviour*, *34*(5), 1359-1371. doi: 10.1016/S0003-3472(86)80207-X

Baptista, L. F., Trail, P. W., DeWolfe, B. B., & Morton, M. L. (1993). Singing and its functions in female white-crowned sparrows. *Animal Behaviour*, *46*(3), 511-524. doi: 10.1006/anbe.1993.1219

Barrington, D. (1773). Xxxi. experiments and observations on the singing of birds, by the hon. daines barrington, vice pres. rs in a letter to mathew maty, md sec. rs. *Philosophical transactions of the Royal Society of London*(63), 249–291. doi: 10.1098/rstl.1773.0031

Bates, D. (2007). Linear mixed-effects models using s4 classes. *http://cran.r-project. org/src/contrib/Descriptions/lme4. html*.

Beecher, M. D. (2008). Function and mechanisms of song learning in song sparrows. *Advances in the Study of Behavior*, *38*, 167-225. doi: 10.1016/S0065-3454(08)00004-1

Beecher, M. D. (2017). Birdsong learning as a social process. *Animal Behaviour*, *124*, 233-246. doi: 10.1016/j.anbehav.2016.09.001

Beecher, M. D., & Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends in Ecology & Evolution*, *20*(3), 143-149. doi: 10.1016/

j.tree.2005.01.004

Beecher, M. D., Stoddard, P. K., Campbell, E. S., & Horning, C. L. (1996). Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, *51*(4), 917-923. doi: 10.1006/anbe.1999.1276

Beletsky, L. D. (1983). Aggressive and pair-bond maintenance songs of female red-winged blackbirds (agelaius pboeniceus). *Zeitschrift für Tierpsychologie*, *62*(1), 47-54. doi: 10.1111/j.1439-0310.1983.tb02140.x

Benedict, L. (2008). Occurrence and life history correlates of vocal duetting in north american passerines. *Journal of Avian Biology*, *39*(1), 57–65.

Berwick, R. C., Okanoya, K., Beckers, G. J., & Bolhuis, J. J. (2011). Songs to syntax: the linguistics of birdsong. *Trends in cognitive sciences*, *15*(3), 113-121. doi: 10.1016/j.tics.2011.01.002

Blondel, J., & Mourer-Chauviré, C. (1998). Evolution and history of the western palaearctic avifauna. *Trends in Ecology & Evolution*, *13*(12), 488–492.

Böhner, J. (1990). Early acquisition of song in the zebra finch, taeniopygia guttata. *Animal Behaviour*, *39*(2), 369-374. doi: 10.1016/S0003-3472(05)80883-8

Boogert, N. J., Lachlan, R. F., Spencer, K. A., Templeton, C. N., & Farine, D. R. (2018). Stress hormones, social associations and song learning in zebra finches. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170290. doi: 10.1098/rstb.2017.0290

Borror, D. J., & Reese, C. R. (1954). Analytical studies of henslow's sparrow songs. *The Wilson Bulletin*, 243-252.

Boughey, M. J., & Thompson, N. S. (1981). Song variety in the brown thrasher (toxostoma rufum). *Zeitschrift für Tierpsychologie*, *56*(1), 47-58. doi: 10.1111/j.1439-0310.1981.tb01283.x

Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature*, *417*(6886), 351. doi: 10.1038/417351a

Brainard, M. S., & Doupe, A. J. (2013). Translating birdsong: songbirds as a model for basic and applied medical research. *Annual review of neuroscience*, *36*, 489-517. doi: 10.1146/annurev-neuro-060909-152826

Brambilla, M., Janni, O., Guidali, F., & Sorace, A. (2008). Song perception among incipient species as a mechanism for reproductive isolation. *Journal of evolutionary biology*, *21*(3), 651-657. doi: 10.1111/j.1420-9101.2008.01523.x

Brenowitz, E. A. (1997). Comparative approaches to the avian song system. *Journal of neurobiology*, *33*(5), 517-531. doi: 10.1002/(SICI)1097-4695(19971105)33:5<517::AID-NEU3>3.0.CO;2-7

Brenowitz, E. A., & Beecher, M. D. (2005). Song learning in birds: diversity and plasticity, opportunities and challenges. *Trends in neurosciences*, *28*(3), 127-132. doi: 10.1016/j.tins.2005.01.004

Briefer, E. F., Rybak, F., & Aubin, T. (2013). Does true syntax or simple auditory object support the role of skylark song dialect? *Animal Behaviour*, *86*(6), 1131-1137. doi: 10.1016/j.anbehav.2013.09.019

Brindley, E. L. (1991). Response of european robins to playback of song: neighbour recognition and overlapping. *Animal Behaviour*, *41*(3), 503-512. doi: 10 .1016/S0003-3472(05)80853-X

Brown, J. L. (1997). A theory of mate choice based on heterozygosity. *Behavioral Ecology*, *8*(1), 60-65. doi: 10.1093/beheco/8.1.60

Brumm, H., Lachlan, R. F., Riebel, K., & Slater, P. J. (2009). On the function of song type repertoires: testing the -antiexhaustion hypothesis in chaffinches. *Animal Behaviour*, *77*(1), 37-42. doi: 10.1016/j.anbehav.2008.09.009

Brumm, H., & Ritschard, M. (2011). Song amplitude affects territorial aggression of male receivers in chaffinches. *Behavioral Ecology*, *22*(2), 310-316. doi: 10.1093/beheco/arq205

Brumm, H., Zollinger, S. A., & Slater, P. J. (2009). Developmental stress affects song learning but not song complexity and vocal amplitude in zebra finches. *Behavioral ecology and sociobiology*, *63*(9), 1387-1395. doi: 10.1007/ s00265-009-0749-y

Bruno, J. H. (2017). *Song rhythm development in zebra finches*. City University of New York.

Bruno, J. H., & Tchernichovski, O. (2017). Regularities in zebra finch song beyond the repeated motif. *Behavioural processes*. doi: 10.1016/j.beproc.2017.11 .001

Buchanan, K. L., Spencer, K. A., Goldsmith, A., & Catchpole, C. K. (2003). Song as an honest signal of past developmental stress in the european starling (sturnus vulgaris). *Proceedings of the Royal Society of London B: Biological Sciences*, *270*(1520), 1149-1156. doi: 10.1016/S0018-506X(03)00124-7

Burt, J. M., Campbell, S. E., & Beecher, M. D. (2001). Song type matching as threat: a test using interactive playback. *Animal Behaviour*, *62*(6), 1163-1170. doi: 10.1006/anbe.2001.1847

Byers, B. E., & Kroodsma, D. E. (2009). Female mate choice and songbird song repertoires. *Animal Behaviour*, *77*(1), 13-22. doi: 10.1016/j.anbehav.2008 .10.003

Carrascal, L. M., Telleria, J. L., & Valido, A. (1992). Habitat distribution of canary chaffinches among islands: competitive exclusion or species-specific habitat preferences? *Journal of Biogeography*, 383-390. doi: 10.2307/2845566

Catchpole, C. K. (1976). Temporal and sequential organisation of song in the sedge warbler (acrocephalus schoenobaenus). *Behaviour*, 226-246. doi: 10.1163/156853976X00370

Catchpole, C. K. (1981). Vocal communication in birds. *Japanese Journal of Ornithology*, *30*(2-3), 87-89. doi: 10.1016/B978-008045046-9.01838-6

Catchpole, C. K. (1987). Bird song, sexual selection and female choice. *Trends in Ecology & Evolution*, *2*(4), 94-97. doi: 10.1016/0169-5347(87)90165-0

Catchpole, C. K., & McGregor, P. K. (1985). Sexual selection, song complexity and plumage dimorphism in european buntings of the genus emberiza. *Animal Behaviour*. doi: 10.1016/S0003-3472(85)80209-8

Catchpole, C. K., & Slater, P. J. (1995). Birdsong: Biological themes and variations. *Cambridge University PressCatchpoleBird song: biological themes and variations1995*.

Catchpole, C. K., & Slater, P. J. (2003). *Bird song: biological themes and variations*. Cambridge university press. doi: 10.1017/CBO9780511754791

Catchpole, C. K., & Slater, P. J. (2008). Bird song: Biological themes and variations.
doi: 10.1017/CBO9780511754791

Cauchoix, M., Hermer, E., Chaine, A., & Morand-Ferron, J. (2017). Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific reports*, *7*(1), 12945. doi: 10.1038/s41598-017-13179-5

Clark, C. W., Marler, P., & Beeman, K. (1987). Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology*, *76*(2), 101-115. doi: 10.1111/j.1439-0310.1987.tb00676.x

Clayton, N. S. P. (1987). Song learning in bengalese finches: a comparison with zebra finches. *Ethology*, *76*(3), 247-255. doi: 10.1111/j.1439-0310.1987.tb00687.x

Clayton, N. S. P. (1989). Song discrimination in female zebra finches and bengalese finches. *Animal Behaviour*, *38*(2), 352-354. doi: 10.1016/S0003-3472(89)80096-X

Clement, P. (1999). *Finches and sparrows* (No. 1). Bloomsbury Publishing. doi: 10.1676/0043-5643(2001)113[0120:ol]2.0.co;2

Collar, N., Newton, I., Clement, P., & Arkhipov, V. (2010). Family fringillidae (finches).

Conrads, K. (1977). Entwicklung einer kombinationsstrophe des buchfinken (fringilla c. coelebs) aus einer grünlings-imitation und arteigenen elementen im freiland. *Bericht der Naturwissenschaftlichen Vereinigung Bielefeld*, *5*, 241-244.

Cooney, R., & Cockburn, A. (1995). Territorial defence is the major function of female song in the superb fairy-wren, malurus cyaneus. *Animal Behaviour*, *49*(6), 1635-1647. doi: 10.1016/0003-3472(95)90086-1

Covas, R. (2011). Evolution of reproductive life histories in island birds worldwide.

Proceedings of the Royal Society B: Biological Sciences, *279*(1733), 1531-1537. doi: 10.1098/rspb.2011.1785

Dahlin, C. R., & Benedict, L. (2014). Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. *Ethology*, *120*(1), 1–10.

Dale, J., Dey, C. J., Delhey, K., Kempenaers, B., & Valcu, M. (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature*, *527*(7578), 367. doi: 10.1038/nature15509

Delgado, A., Calabuig, P., Suárez, V., Trujillo, D., & Suárez-Rancel, M. M. (2016). Preliminary assessment of the release of captive-bred gran canaria blue chaffinches fringilla teydea polatzeki as a reinforcement population. *Bird Study*, *63*(4), 554-558. doi: 10.1080/00063657.2016.1239694

del Hoyo, J., Elliott, A., & Christie, D. (2011). Handbook of the birds of the world. vol. 15. weavers to new world warblers. *British Birds*, *104*, 225-8.

Dennison, M. D. (1991). *Morphometric and ecological differentiation of atlantic island chaffinch (" fringilla" spp.) populations* (Unpublished doctoral dissertation).

Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Aleixo, A., & Brumfield, R. T. (2012). Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution: International Journal of Organic Evolution*, *66*(9), 2784-2797. doi: 10.1111/j.1558-5646.2012.01642.x

DeWolfe, B. B., Baptista, L. F., & Petrinovich, L. (1989). Song development and territory establishment in nuttall's white-crowned sparrows. *The Condor*, *91*(2), 397-407. doi: 10.2307/1368318

Dhawale, A. K., Smith, M. A., & Ölveczky, B. P. (2017). The role of variability in motor learning. *Annual review of neuroscience*, *40*, 479-498. doi: 10.11606/issn.2594-5904.rpef.2000.139613

Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: common themes and mechanisms. *Annual review of neuroscience*, *22*(1), 567-631. doi: 10.1146/annurev.neuro.22.1.567

Dowling, J. L., Colombelli-Négrel, D., & Webster, M. S. (2016). Kin signatures learned in the egg? red-backed fairy-wren songs are similar to their mother's in-nest calls and songs. *Frontiers in Ecology and Evolution*, *4*, 48. doi: 10.3389/fevo.2016.00048

Drăgănoiu, T. I., Nagle, L., & Kreutzer, M. (2002). Directional female preference for an exaggerated male trait in canary (serinusanaria) song. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1509), 2525-2531. doi: 10.1098/rspb.2002.2192

Eales, L. A. (1985). Song learning in zebra finches: some effects of song model

availability on what is learnt and when. *Animal Behaviour*, *33*(4), 1293-1300. doi: 10.1016/S0003-3472(85)80189-5

Ebenman, B., & Nilsson, S. G. (1982). Components of niche width in a territorial bird species: habitat utilization in males and females of the chaffinch (*Fringilla coelebs*) on islands and mainland. *The American Naturalist*, *119*(3), 331-344. doi: 10.1086/283913

Eens, M., Pinxten, R., & Verheyen, R. F. (1992). Song learning in captive european starlings, sturnus vulgaris. *Animal Behaviour*, *44*(6), 1131-1143. doi: 10.1016/S0003-3472(05)80325-2

Eriksson, D., & Wallin, L. (1986). Male bird song attracts females-a field experiment. *Behavioral Ecology and Sociobiology*, *19*(4), 297-299. doi: 10.1007/BF00300645

Farabaugh, S. M., Brown, E. D., & Veltman, C. J. (1988). Song sharing in a group-living songbird, the australian magpie: Ii. vocal sharing between territorial neighbors, within and between geographic regions, and between sexes. *Behaviour*. doi: 10.1163/156853988X00629

Fedy, B. C., & Stutchbury, B. J. (2005). Territory defence in tropical birds: are females as aggressive as males? *Behavioral Ecology and Sociobiology*, *58*(4), 414-422. doi: 10.1007/s00265-005-0928-4

Fee, M. S., Kozhevnikov, A. A., & Hahnloser, R. H. (2004). Neural mechanisms of vocal sequence generation in the songbird. *Annals of the New York Academy of Sciences*, *1016*(1), 153-170. doi: 10.1196/annals.1298.022

Fernández-Palacios, J. M., de Nascimento, L., Otto, R., Delgado, J. D., García-del Rey, E., Arévalo, J. R., & Whittaker, R. J. (2011). A reconstruction of palaeo-macaronesia, with particular reference to the long-term biogeography of the atlantic island laurel forests. *Journal of Biogeography*, *38*(2), 226-246. doi: 10.1111/j.1365-2699.2010.02427.x

Frankham, R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity*, *78*(3), 311. doi: 10.1038/hdy.1997.46

Gahr, M. (2000). Neural song control system of hummingbirds: comparison to swifts, vocal learning (songbirds) and nonlearning (suboscines) passerines, and vocal learning (budgerigars) and nonlearning (dove, owl, gull, quail, chicken) nonpasserines. *Journal of Comparative Neurology*, *426*(2), 182-196. doi: 10.1002/1096-9861(20001016)426:2<182::AID-CNE2>3.0.CO;2-M

Garamszegi, L. Z., Pavlova, D. Z., Eens, M., & Møller, A. P. (2007). The evolution of song in female birds in europe. *Behavioral Ecology*, *18*(1), 86-96. doi: 10.1093/beheco/arl047

Garcia-del Rey, E. (2011). Field guide to the birds of macaronesia. *Azores, Madeira, Canary Islands, Cape Verde. Lynx Edicions, Bellaterra, Barcelona.*

doi: 10.2307/3536354

Garcia-del Rey, E. (2018). *Birds of the canary islands*. Bloomsbury Publishing.

Garcia-del Rey, E., & Cresswell, W. (2005). Density estimates, microhabitat selection and foraging behaviour of the endemic blue chaffinch fringilla teydea teydea on tenerife (canary islands). *Ardeola*, *52*(2), 305-317.

García-Del-Rey, E., & Gosler, A. G. (2005). Biometrics, ageing, sexing and moult of the blue chaffinch fringilla teydea teydea on tenerife (canary islands). *Ringing & Migration*, *22*(3), 177-184.

Geberzahn, N., & Hultsch, H. (2004). Rules of song development and their use in vocal interactions by birds with large repertoires. *Anais da Academia Brasileira de Ciências*, *76*(2), 209-218. doi: 10.1590/S0001-37652004000200004

Gil, D., Cobb, J. L., & Slater, P. J. (2001). Song characteristics are age dependent in the willow warbler, phylloscopus trochilus. *Animal Behaviour*, *62*(4), 689-694. doi: 10.1006/anbe.2001.1812

Goodfellow, D., & Slater, P. J. (1986). A model of bird song dialects. *Animal Behaviour*. doi: 10.1016/S0003-3472(86)80233-0

Grafe, T. U., & Bitz, J. H. (2004). Functions of duetting in the tropical boubou, laniarius aethiopicus: territorial defence and mutual mate guarding. *Animal Behaviour*, *68*(1), 193-201. doi: 10.1016/j.anbehav.2003.11.003

Grant, P. R. (1979). Evolution of the chaffinch, *Fringilla coelebs*, on the atlantic islands. *Biological Journal of the Linnean Society*, *11*(4), 301-332. doi: 10.1111/j.1095-8312.1979.tb00042.x

Grant, P. R. (1998). *Evolution on islands*. Oxford University Press, USA.

Griffith, S. C., Stewart, I. R., Dawson, D. A., Owens, I. P., & Burke, T. (1999). Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (passer domesticus): is there an "island effect"? *Biological Journal of the Linnean society*, *68*(1-2), 303-316. doi: 10.1006/bijl.1999.0343

Griswold, C. K., & Baker, A. J. (2002). Time to the most recent common ancestor and divergence times of populations of common chaffinches (*Fringilla coelebs*) in europe and north africa: insights into pleistocene refugia and current levels of migration. *Evolution*, *56*(1), 143-153. doi: 10.1111/j.0014-3820.2002.tb00856.x

Güttinger, H. R. (1985). Consequences of domestication on the song structures in the canary. *Behaviour*, 254–278.

Hadfield, J. D. (2010). Mcmc methods for multi-response generalized linear mixed models: the mcmcglmm r package. *Journal of Statistical Software*, *33*(2), 1-22. doi: 10.18637/jss.v033.i02

Hahnloser, R. H., Kozhevnikov, A. A., & Fee, M. S. (2002). An ultra-sparse

code underliesthe generation of neural sequences in a songbird. *Nature*, *419*(6902), 65. doi: 10.1038/nature01221

Hall, M. L. (2000). The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour*, *60*(5), 667-677. doi: 10.1006/anbe.2000.1517

Hall, M. L. (2009). A review of vocal duetting in birds. *Advances in the Study of Behavior*, *40*, 67-121. doi: 10.1016/S0065-3454(09)40003-2

Hall, M. L., & Langmore, N. E. (2017). Fitness costs and benefits of female song. *Frontiers in Ecology and Evolution*, *5*, 48. doi: 10.3389/fevo.2017.00048

Hall, M. L., Rittenbach, M. R., & Vehrencamp, S. L. (2015). Female song and vocal interactions with males in a neotropical wren. *Frontiers in Ecology and Evolution*, *3*, 12. doi: 10.3389/fevo.2015.00012

Halliday, H. (1948). Song of female chaffinch. *Brit. Birds*, *41*, 343-4.

Hamao, S., & Ueda, K. (2000). Simplified song in an island population of the bush warbler cettia diphone. *Journal of Ethology*, *18*(1), 53-57. doi: 10.1007/s101640070025

Hansen, P. (1979). Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*. doi: 10.1016/0003-3472(79)90073-3

Hanski, I. K., & Laurila, A. (1993). Variation in song rate during the breeding cycle of the chaffinch, *Fringilla coelebs*. *Ethology*, *93*(2), 161-169. doi: 10.1111/j.1439-0310.1993.tb00986.x

Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-term persistence of song dialects in the mountain white-crowned sparrow. *The Condor*, *101*(1), 133-148. doi: 10.2307/1370454

Hartwig, S. (2005). Individual acoustic identification as a non-invasive conservation tool: an approach to the conservation of the african wild dog lycaon pictus (temminck, 1820). *Bioacoustics*, *15*(1), 35-50. doi: 10.1080/09524622.2005.9753537

Hathcock, T., & Benedict, L. (2018). Conspecific challenges provoke female canyon wrens to sing but not to duet. *Behavioral ecology and sociobiology*, *72*(12), 196.

Hausberger, M., & Black, J. M. (1991). Female song in european starlings: the case of non-competitive song-matching. *Ethology ecology & evolution*, *3*(4), 337-344. doi: 10.1080/08927014.1991.9525362

Hinde, R. (1958). Alternative motor patterns in chaffinch song. *Animal Behaviour*, *6*(3-4), 211-218. doi: 10.1016/0003-3472(58)90053-8

Hobson, K. A., & Sealy, S. G. (1990). Female song in the yellow warbler. *The Condor*, *92*(1), 259-261. doi: 10.2307/1368416

Hoese, W. J., Podos, J., Boetticher, N. C., & Nowicki, S. (2000). Vocal tract function in birdsong production: experimental manipulation of beak movements. *Journal of Experimental Biology*, *203*(12), 1845-1855.

Holveck, M.-J., Vieira de Castro, A. C., Lachlan, R. F., ten Cate, C., & Riebel, K. (2008). Accuracy of song syntax learning and singing consistency signal early condition in zebra finches. *Behavioral Ecology*, *19*(6), 1267-1281. doi: 10.1093/beheco/arn078

Honda, E., & Okanoya, K. (1999). Acoustical and syntactical comparisons between songs of the white-backed munia (lonchura striata) and its domesticated strain, the bengalese finch (lonchura striata var. domestica). *Zoological Science*, *16*(2), 319-327. doi: 10.2108/zsj.16.319

Huber, S. K., & Podos, J. (2006). Beak morphology and song features covary in a population of darwin's finches (geospiza fortis). *Biological Journal of the Linnean Society*, *88*(3), 489-498. doi: 10.1111/j.1095-8312.2006.00638.x

Hughes, M., Nowicki, S., Searcy, W. A., & Peters, S. (1998). Song-type sharing in song sparrows: implications for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, *42*(6), 437-446. doi: 10.1007/s002650050458

Hultsch, H. (1991). Early experience can modify singing styles: evidence from experiments with nightingales, luscinia megarhynchos. *Animal Behaviour*, *42*(6), 883-889. doi: 10.1016/S0003-3472(05)80140-X

Hultsch, H., & Todt, D. (1989). Memorization and reproduction of songs in nightingales (luscinia megarhynchos): evidence for package formation. *Journal of Comparative Physiology A*, *165*(2), 197-203. doi: 10.1007/BF00619194

Hultsch, H., & Todt, D. (1996). Rules of parameter variation in homotype series of birdsong can indicate a -sollwert-significance. *Behavioural processes*, *38*(2), 175-182. doi: 10.1016/S0376-6357(96)00021-6

Hwang, W.-J., & Wen, K.-W. (1998). Fast knn classification algorithm based on partial distance search. *Electronics letters*, *34*(21), 2062-2063. doi: 10.1049/el:19981427

Illera, J. C., Rando, J. C., Rodriguez-Exposito, E., Hernández, M., Claramunt, S., & Martín, A. (2018). Acoustic, genetic, and morphological analyses of the canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification. *Journal of Avian Biology*, *49*(12). doi: 10.1111/jav.01885

Illes, A. E., & Yunes-Jimenez, L. (2008). A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1658), 981-986. doi: 10.1098/rspb.2008.1445

Immelmann, K. (1969). Song development in the zebra finch and other estrildid finches. *Bird vocalizations*, 61-77.

Ince, S., Slater, P. J., & Band Weismann, C. (1980). Changes with time in the songs of a population of chaffinches. *The Condor*, *82*(3), 285-290. doi: 10.2307/1367393

Irwin, D. E. (2000). Song variation in an avian ring species. *Evolution*, *54*(3), 998-1010. doi: 10.1111/j.0014-3820.2000.tb00099.x

Janik, V. M., & Slater, P. J. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, 59-100. doi: 10.1016/S0065-3454(08)60377-0

Jarvis, E. D. (2004). Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Sciences*, *1016*(1), 749-777. doi: 10.1196/annals.1298.038

Jones, A., & Slater, P. J. (1996). The role of aggression in song tutor choice in the zebra finch: cause or effect? *Behaviour*, *133*(1-2), 103-115. doi: 10.1163/156853996X00053

Järvi, T., Radesäter, T., & Jakobsson, S. (1980). The song of the willow warbler phylloscopus trochilus with special reference to singing behaviour in agonistic situations. *Ornis Scandinavica*, 236-242. doi: 10.2307/3676129

Kahle, D., & Wickham, H. (2013). ggmap: Spatial visualization with ggplot2. *The R Journal*, *5*(1), 144–161. Retrieved from `https://journal.r-project.org/archive/2013-1/kahle-wickham.pdf`

Kirn, J. R. (2010). The relationship of neurogenesis and growth of brain regions to song learning. *Brain and language*, *115*(1), 29-44. doi: 10.1016/j.bandl.2009.09.006

Klicka, J., Barker, F. K., Burns, K. J., Lanyon, S. M., Lovette, I. J., Chaves, J. A., & Bryson Jr, R. W. (2014). A comprehensive multilocus assessment of sparrow (aves: Passerellidae) relationships. *Molecular Phylogenetics and Evolution*, *77*, 177-182. doi: 10.1016/j.ympev.2014.04.025

Kling, J., & Stevenson-Hinde, J. (1977). Development of song and reinforcing effects of song in female chaffinches. *Animal behaviour*, *25*, 215-220. doi: 10.1016/0003-3472(77)90084-7

Koloff, J., & Mennill, D. (2011). Aggressive responses to playback of solos and duets in a neotropical antbird. *Animal Behaviour*, *82*(3), 587-593. doi: 10.1016/j.anbehav.2011.06.021

Koloff, J., & Mennill, D. J. (2013). The responses of duetting antbirds to stereo duet playback provide support for the joint territory defence hypothesis. *Ethology*, *119*(6), 462-471. doi: 10.1111/eth.12084

Konishi, M. (1964). Effects of deafening on song development in two species of juncos. *The Condor*, *66*(2), 85-102. doi: 10.2307/1365388

Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift fur Tierpsychologie*, *22*(7), 770.

doi: 10.1111/j.1439-0310.1965.tb01688.x

Konishi, M. (1985). Birdsong: from behavior to neuron. *Annual review of neuroscience*, *8*(1), 125-170. doi: 10.1146/annurev.neuro.8.1.125

Konishi, M. (2004). The role of auditory feedback in birdsong. *Annals of the New York Academy of Sciences*, *1016*(1), 463-475. doi: 10.1196/annals.1298.010

Krebs, J. R., Ashcroft, R., & Van Orsdol, K. (1981). Song matching in the great tit parus major l. *Animal Behaviour*, *29*(3), 918-923. doi: 10.1016/S0003-3472(81)80029-2

Krieg, C. A., & Getty, T. (2016). Not just for males: females use song against male and female rivals in a temperate zone songbird. *Animal Behaviour*, *113*, 39-47. doi: 10.1016/j.anbehav.2015.12.019

Kriner, E., & Schwabl, H. (1991). Control of winter song and territorial aggression of female robins (erithacus rubecula) by testosterone. *Ethology*, *87*(1-2), 37-44. doi: 10.1111/j.1439-0310.1991.tb01186.x

Kroodsma, D. E. (1986). Design of song playback experiments. *The Auk*, *103*(3), 640-642.

Kroodsma, D. E. (2004). The diversity and plasticity of birdsong. *Nature's music: the science of birdsong*, 108–131. doi: 10.1016/B978-012473070-0/50007-4

Kroodsma, D. E., Albano, D. J., Houlihan, P. W., & Wells, J. A. (1995). Song development by black-capped chickadees (parus atricapillus) and carolina chickadees (p. carolinensis). *The Auk*, *112*(1), 29-43. doi: 10.2307/4088764

Kroodsma, D. E., & Baylis, J. (1982). Appendix: a world survey of evidence for vocal learning in birds. *Acoustic communication in birds*, *2*, 311-337.

Kroodsma, D. E., Byers, B. E., Halkin, S. L., Hill, C., Minis, D., Bolsinger, J. R., ... Gill, F. B. (1999). Geographic variation in black-capped chickadee songs and singing behavior. *The Auk*, *116*(2), 387-402. doi: 10.2307/4089373

Kroodsma, D. E., Houlihan, P. W., Fallon, P. A., & Wells, J. A. (1997). Song development by grey catbirds. *Animal behaviour*, *54*(2), 457–464.

Kroodsma, D. E., Ingalls, V. A., Sherry, T. W., & Werner, T. K. (1987). Songs of the cocos flycatcher: vocal behavior of a suboscine on an isolated oceanic island. *The Condor*, *89*(1), 75-84. doi: 10.2307/1368761

Kroodsma, D. E., & Miller, E. (1996). Ecology and evolution of acoustic communication in birds pp. 269-281. *Comstock Pub.* doi: 10.2307/2266158

Kroodsma, D. E., Miller, E. H., & Ouellet, H. (1982). *Acoustic communication in birds: Song learning and its consequences* (Vol. 2). Academic press.

Kuhl, P. K. (2004). Early language acquisition: cracking the speech code. *Nature reviews neuroscience*, *5*(11), 831. doi: 10.1038/nrn1533

Kunkel, G. (2012). *Biogeography and ecology in the canary islands* (Vol. 30). Springer Science & Business Media. doi: 10.2307/1796692

Lachlan, R. F., Anderson, R., Peters, S., Searcy, W., & Nowicki, S. (2014). Typical versions of learned swamp sparrow song types are more effective signals than are less typical versions. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1785), 20140252. doi: 10.1098/rspb.2014.0252

Lachlan, R. F., & Feldman, M. W. (2003). Evolution of cultural communication systems: the coevolution of cultural signals and genes encoding learning preferences. *Journal of evolutionary biology*, *16*(6), 1084-1095. doi: 10.1046/j.1420-9101.2003.00624.x

Lachlan, R. F., Janik, V. M., & Slater, P. J. (2004). The evolution of conformity-enforcing behaviour in cultural communication systems. *Animal Behaviour*, *68*(3), 561-570. doi: 10.1016/j.anbehav.2003.11.015

Lachlan, R. F., & Nowicki, S. (2012). How reliable is song learning accuracy as a signal of male early condition? *American Naturalist*, *180*(6), 751-761. doi: 10.1086/668010

Lachlan, R. F., Ratmann, O., & Nowicki, S. (2018). Cultural conformity generates extremely stable traditions in bird song. *Nature communications*, *9*(1), 2417. doi: 10.1038/s41467-018-04728-1

Lachlan, R. F., & Servedio, M. R. (2004). Song learning accelerates allopatric speciation. *Evolution*, *58*(9), 2049-2063.

Lachlan, R. F., & Slater, P. J. B. (1999). The maintenance of vocal learning by gene-culture interaction: the cultural trap hypothesis. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1420), 701-706. doi: 10.1098/rspb.1999.0692

Lachlan, R. F., & Slater, P. J. B. (2003). Song learning by chaffinches: how accurate, and from where? *Animal Behaviour*, *65*(5), 957-969. doi: 10.1006/anbe.2003.2091

Lachlan, R. F., Van Heijningen, C. A., Ter Haar, S. M., & Ten Cate, C. (2016). Zebra finch song phonology and syntactical structure across populations and continents-a computational comparison. *Frontiers in psychology*, *7*, 980. doi: 10.3389/fpsyg.2016.00980

Lachlan, R. F., Verhagen, L., Peters, S., & Cate, C. t. (2010). Are there species-universal categories in bird song phonology and syntax? a comparative study of chaffinches (*Fringilla coelebs*), zebra finches (*Taenopygia guttata*), and swamp sparrows (*Melospiza georgiana*). *Journal of Comparative Psychology*, *124*(1), 92. doi: 10.1037/a0016996

Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P.-P., Koese, B., Jaarsma, S., ... ten Cate, C. (2013). The progressive loss of syntactical structure in bird song along an island colonization chain. *Current Biology*, *23*(19), 1896-1901. doi: 10.1016/j.cub.2013.07.057

Lack, D. (1943). Notes on territory, fighting and display in the chaffinch. *British Birds*, *34*, 216-219.

Lack, D., & Southern, H. (1949). Birds on tenerife. *Ibis*, *91*(4), 607-626. doi: 10.1111/j.1474-919X.1949.tb02313.x

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4-14.

Langmore, N. E. (1998). Functions of duet and solo songs of female birds. *Trends Ecol Evol*, *13*(4), 136-40. doi: 10.1016/S0169-5347(97)01241-X

Langmore, N. E., Davies, N., Hatchwell, B., & Hartley, I. (1996). Female song attracts males in the alpine accentor prunella collaris. *Proc. R. Soc. Lond. B*, *263*(1367), 141-146. doi: 10.1098/rspb.1996.0022

Leitão, A., & Riebel, K. (2003). Are good ornaments bad armaments? male chaffinch perception of songs with varying flourish length. *Animal Behaviour*, *66*(1), 161-167. doi: 10.1006/anbe.2003.2167

Leitner, S., Nicholson, J., Leisler, B., DeVoogd, T. J., & Catchpole, C. K. (2002). Song and the song control pathway in the brain can develop independently of exposure to song in the sedge warbler. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1509), 2519–2524.

Leitner, S., Teichel, J., Ter Maat, A., & Voigt, C. (2015). Hatching late in the season requires flexibility in the timing of song learning. *Biology letters*, *11*(8), 20150522.

Leitão, A., Ten Cate, C., & Riebel, K. (2006). Within-song complexity in a songbird is meaningful to both male and female receivers. *Animal Behaviour*, *71*(6), 1289-1296. doi: 10.1016/j.anbehav.2005.08.008

Lemon, R. E. (1975). How birds develop song dialects. *The Condor*, *77*(4), 385-406. doi: 10.2307/1366087

Levin, R. N. (1996). Song behaviour and reproductive strategies in a duetting wren,thryothorus nigricapillus: Ii. playback experiments. *Animal Behaviour*, *52*(6), 1107-1117. doi: 10.1006/anbe.1996.0257

Lifjeld, J. T., Anmarkrud, J. A., Calabuig, P., Cooper, J. E., Johannessen, L. E., Johnsen, A., ... Marthinsen, G. (2016). Species-level divergences in multiple functional traits between the two endemic subspecies of blue chaffinches fringilla teydea in canary islands. *BMC Zoology*, *1*(1), 4. doi: 10.1186/s40850-016-0008-4

Lipkind, D., Marcus, G. F., Bemis, D. K., Sasahara, K., Jacoby, N., Takahasi, M., ... Okanoya, K. (2013). Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature*, *498*(7452), 104. doi: 10.1038/nature12173

Lipkind, D., Zai, A. T., Hanuschkin, A., Marcus, G. F., Tchernichovski, O.,

& Hahnloser, R. H. (2017). Songbirds work around computational complexity by learning song vocabulary independently of sequence. *Nature communications*, *8*(1), 1247. doi: 10.1038/s41467-017-01436-0

Liu, W., Gardner, T. J., & Nottebohm, F. (2004). Juvenile zebra finches can use multiple strategies to learn the same song. *Proceedings of the National Academy of Sciences*, *101*(52), 18177-18182. doi: 10.1073/pnas.0408065101

Liu, W., & Kroodsma, D. E. (2006). Song learning by chipping sparrows: when, where, and from whom. *The Condor*, *108*(3), 509-517. doi: 10.1016/S0252-9602(06)60076-3

Lombardino, A. J., & Nottebohm, F. (2000). Age at deafening affects the stability of learned song in adult male zebra finches. *Journal of Neuroscience*, *20*(13), 5054-5064.

Long, M. A., & Fee, M. S. (2008). Using temperature to analyse temporal dynamics in the songbird motor pathway. *Nature*, *456*(7219), 189. doi: 10.1038/nature07448

Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, *457*(7231), 830. doi: 10.1038/nature07893

Lynch, A., & Baker, A. J. (1991). Increased vocal discrimination by learning in sympatry in two species of chaffinches. *Behaviour*, *116*(1), 109-125.

Lynch, A., & Baker, A. J. (1993). A population memetics approach to cultural evolution in chaffinch song: meme diversity within populations. *The American Naturalist*, *141*(4), 597-620. doi: 10.1086/285493

Lynch, A., & Baker, A. J. (1994). A population memetics approach to cultural evolution in chaffinch song: differentiation among populations. *Evolution*, *48*(2), 351-359.

MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, *53*(2), 330-342.

Magoolagan, L., Mawby, P. J., Whitehead, F. A., & Sharp, S. P. (2019). The structure and context of male and female song in white-throated dippers. *Journal of ornithology*, *160*(1), 195-205. doi: 10.1007/s10336-018-1599-z

Malacarne, G., Cucco, M., & Camanni, S. (1991). Coordinated visual displays and vocal duetting in different ecological situations among western palearctic non-passerine birds. *Ethology ecology & evolution*, *3*(3), 207–219.

Mann, N. I., & Slater, P. J. (1995). Song tutor choice by zebra finches in aviaries. *Animal Behaviour*, *49*(3), 811-820. doi: 10.1016/0003-3472(95)80212-6

Marjakangas, A. (1981). A singing chaffinch *Fringilla coelebs* in female plumage paired with another female-plumaged chaffinch. *Ornis Fennica*, *58*, 90-91.

Marler, P. (1952). Variation in the song of the chaffinch *Fringilla coelebs*. *Ibis*, *94*(3), 458-472. doi: 10.1111/j.1474-919X.1952.tb01845.x

Marler, P. (1956a). Behaviour of the chaffinch *Fringilla coelebs*. *Behaviour. Supplement*, III-184. doi: 10.2307/4510692

Marler, P. (1956b). Territory and individual distance in the chaffinch *Fringilla coelebs*. *Ibis*, *98*(3), 496-501. doi: 10.2307/4510692

Marler, P. (1956c). The voice of the chaffinch and its function as a language. *Ibis*, *98*(2), 231-261. doi: 10.1111/j.1474-919X.1956.tb03042.x

Marler, P. (1958). Bird songs and mate selection. *Animal Behaviour*, *6*(3-4), 254. doi: 10.1016/0003-3472(58)90090-3

Marler, P. (1970). A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of comparative and physiological psychology*, *71*(2p2), 1. doi: 10.1037/h0029144

Marler, P. (2004). Bird calls: a cornucopia for communication. In *Nature's music* (p. 132-177). Elsevier. doi: 10.1016/B978-012473070-0/50008-6

Marler, P., & Boatman, D. J. (1951). Observations on the birds of pico, azores. *Ibis*, *93*(1), 90-99. doi: 10.1111/j.1474-919X.1961.tb02456.x

Marler, P., & Peters, S. (1977). Selective vocal learning in a sparrow. *Science*, *198*(4316), 519-521. doi: 10.1126/science.198.4316.519

Marler, P., & Peters, S. (1981). Sparrows learn adult song and more from memory. *Science*, *213*(4509), 780-782. doi: 10.1126/science.213.4509.780

Marler, P., & Peters, S. (1982). Developmental overproduction and selective attrition: new processes in the epigenesis of birdsong. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *15*(4), 369-378. doi: 10.1002/dev.420150409

Marler, P., & Peters, S. (1987). A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*: a case of age-limited learning. *Ethology*, *76*(2), 89-100. doi: 10.1111/j.1439-0310.1987.tb00675.x

Marler, P., & Peters, S. (1988). The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*. *Ethology*, *77*(2), 125-149. doi: 10.1111/j.1439-0310.1988.tb00198.x

Marler, P., Peters, S., Ball, G. F., Dufty Jr, A. M., & Wingfield, J. C. (1988). The role of sex steroids in the acquisition and production of birdsong. *Nature*, *336*(6201), 770. doi: 10.1038/336770a0

Marler, P., & Sherman, V. (1985). Innate differences in singing behaviour of sparrows reared in isolation from adult conspecific song. *Animal Behaviour*, *33*(1), 57-71. doi: 10.1016/S0003-3472(85)80120-2

Marler, P., & Tamura, M. (1962). Song 'dialects' in three populations of white-crowned sparrows. *The Condor*, *64*(5), 368-377. doi: 10.2307/1365545

Marshall, H. D., & Baker, A. J. (1999). Colonization history of atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial dna. *Molecular*

Phylogenetics and Evolution, *11*(2), 201-212. doi: 10.1006/mpev.1998.0552

Marshall, H. D., Baker, A. J., & Grant, A. R. (2013). Complete mitochondrial genomes from four subspecies of common chaffinch (fringilla coelebs): new inferences about mitochondrial rate heterogeneity, neutral theory, and phylogenetic relationships within the order passeriformes. *Gene*, *517*(1), 37–45.

Martin, P. R., Fotheringham, J. R., Ratcliffe, L., & Robertson, R. J. (1996). Response of american redstarts (suborder passeri) and least flycatchers (suborder tyranni) to heterospecific playback: the role of song in aggressive interactions and interference competition. *Behavioral Ecology and Sociobiology*, *39*(4), 227–235.

Martin, P. R., & Martin, T. E. (2001). Behavioral interactions between coexisting species: song playback experiments with wood warblers. *Ecology*, *82*(1), 207-218. doi: 10.1006/mpev.1998.0552

Mason, N. A., Pasch, B., Burns, K. J., & Derryberry, E. P. (2017). Integrating museum and media collections to study vocal ecology and evolution 1. In *The extended specimen* (pp. 57–74). CRC Press. doi: 10.1201/9781315120454

Matthews, A. E., Slevin, M. C., Worm, A. J., & Boves, T. J. (2017). Female prothonotary warblers protonotaria citrea sing during the mate acquisition period. *Ibis*, *159*(1), 221-224. doi: 10.1111/ibi.12421

McArthur, P. D., Peters, S. S., Searcy, W. A., & Marler, P. (1981). Response of male song and swamp sparrows to neighbour, stranger, and self songs. *Behaviour*, *77*(3), 152-163. doi: 10.1163/156853981X00202

McGregor, P. K. (1992). Quantifying responses to playback: one, many, or composite multivariate measures? In *Playback and studies of animal communication* (pp. 79–96). Springer.

McGregor, P. K. (2000). Playback experiments: design and analysis. *Acta ethologica*, *3*(1), 3-8.

McGregor, P. K. (2005). *Animal communication networks*. Cambridge University Press. doi: 10.1017/CBO9780511610363

McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, H. C., ... Kroodsma, D. E. (1992). Design of playback experiments: the thornbridge hall nato arw consensus. In *Playback and studies of animal communication* (p. 1-9). Springer. doi: 10.1007/978-1-4757-6203-7_1

Mennill, D. J. (2006). Aggressive responses of male and female rufous-and-white wrens to stereo duet playback. *Animal Behaviour*, *71*(1), 219-226. doi: 10.1016/j.anbehav.2005.05.006

Mennill, D. J., Doucet, S. M., Newman, A. E., Williams, H., Moran, I. G., Thomas, I. P., ... Norris, D. R. (2018). Wild birds learn songs from

experimental vocal tutors. *Current Biology*, *28*(20), 3273-3278. e4. doi: 10.1016/j.cub.2018.08.011

Mennill, D. J., & Vehrencamp, S. L. (2008). Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. *Current Biology*, *18*(17), 1314-1319. doi: 10.1016/j.cub.2008.07.073

Metzmacher, M. (1982). A propos de similitudes de structure dans le chant du pinson des arbres *Fringilla coelebs* de différentes populations. *Le Gerfaut, Revue belge d'ornithologie= De Giervalk, Belgisch Ornithologisch Tijdschrift*, *72*, 73-75.

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: associative learning in wild great tits. *PloS one*, *10*(8), e0133821. doi: 10.1371/journal.pone.0133821

Morinay, J., Cardoso, G. C., Doutrelant, C., & Covas, R. (2013). The evolution of birdsong on islands. *Ecology and evolution*, *3*(16), 5127-5140. doi: 10.1002/ece3.864

Mountjoy, J. D., & Lemon, R. E. (1995). Extended song learning in wild european starlings. *Animal Behaviour*, *49*(2), 357-366. doi: 10.1016/j.anbehav.2016.05.011

Mundinger, P. C. (1995). Behaviour-genetic analysis of canary song: inter-strain differences in sensory learning, and epigenetic rules. *Animal Behaviour*, *50*(6), 1491-1511. doi: 10.1007/s00265-010-0989-x

Müller, W., Vergauwen, J., & Eens, M. (2010). Testing the developmental stress hypothesis in canaries: consequences of nutritional stress on adult song phenotype and mate attractiveness. *Behavioral ecology and sociobiology*, *64*(11), 1767-1777. doi: 10.1006/anbe.1995.0048

Nelson, D. A. (1992a). Song overproduction and selective attrition lead to song sharing in the field sparrow (spizella pusilla). *Behavioral Ecology and Sociobiology*, *30*(6), 415-424. doi: 10.1007/BF00176177

Nelson, D. A. (1992b). Song overproduction, song matching and selective attrition during development. In *Playback and studies of animal communication* (p. 121-133). Springer. doi: 10.1007/978-1-4757-6203-7_9

Nelson, D. A. (1999). Ecological influences on vocal development in the white-crowned sparrow. *Animal Behaviour*, *58*(1), 21-36. doi: 10.1006/anbe.1999.1118

Nelson, D. A. (2000). Song overproduction, selective attrition and song dialects in the white-crowned sparrow. *Animal Behaviour*, *60*(6), 887-898. doi: 10.1006/anbe.2000.1560

Nelson, D. A., Marler, P., & Morton, M. L. (1996). Overproduction in song development: an evolutionary correlate with migration. *Animal Behaviour*,

51(5), 1127-1140. doi: 10.1006/anbe.1996.0114

Nelson, D. A., Marler, P., & Palleroni, A. (1995). A comparative approach to vocal learning: intraspecific variation in the learning process. *Animal Behaviour*, *50*(1), 83-97. doi: 10.1006/anbe.1995.0223

Nemeth, E., Kempenaers, B., Matessi, G., & Brumm, H. (2012). Rock sparrow song reflects male age and reproductive success. *PLoS One*, *7*(8), e43259. doi: 10.1371/journal.pone.0043259

Newton, I. (1964). The breeding biology of the chaffinch. *Bird Study*, *11*(1), 47-68. doi: 10.1080/00063655409475783

Nice, M. M. (1941). The role of territory in bird life. *American Midland Naturalist*, 441-487. doi: 10.2307/2420732

Nicholson, E. M. (1931). *The art of bird-watching: a practical guide to field observation*. HF & G. Witherby.

Nol, E., & Smith, J. N. (1987). Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *The Journal of Animal Ecology*, 301-313. doi: 10.2307/4816

Nordby, J. C., Campbell, S. E., & Beecher, M. D. (2007). Selective attrition and individual song repertoire development in song sparrows. *Animal Behaviour*, *74*(5), 1413-1418. doi: 10.1016/j.anbehav.2007.02.008

Norton, P., & Scharff, C. (2016). -bird song metronomics-: isochronous organization of zebra finch song rhythm. *Frontiers in neuroscience*, *10*, 309. doi: 10.3389/fnins.2016.00309

Nottebohm, F. (1967). *The role of sensory feedback in the development of avian vocalizations* (Unpublished doctoral dissertation).

Nottebohm, F. (1968). Auditory experience and song development in the chaffinch *Fringilla coelebs*. *Ibis*, *110*(4), 549-568. doi: 10.1111/j.1474-919X.1968.tb00063.x

Nottebohm, F. (1969a). The 'critical period' for song learning. *Ibis*, *111*(3), 386-387. doi: 10.1111/j.1474-919X.1969.tb02551.x

Nottebohm, F. (1969b). The song of the chingolo, zonotrichia capensis, in argentina: Description and evaluation of a system of dialects. *The Condor*, *71*(3), 299-315. doi: 10.2307/1366306

Nottebohm, F. (1970). Ontogeny of bird song. *Science*, *167*(3920), 950-956. doi: 10.1126/science.167.3920.950

Nottebohm, F. (1972a). Neural lateralization of vocal control in a passerine bird. ii. subsong, calls, and a theory of vocal learning. *Journal of Experimental Zoology*, *179*(1), 35-49. doi: 10.1002/jez.1401790104

Nottebohm, F. (1972b). The origins of vocal learning. *The American Naturalist*, *106*(947), 116-140. doi: 10.1086/282756

Nottebohm, F. (1992). The search for neural mechanisms that define the sensitive period for song learning in birds. *Netherlands Journal of Zoology*, *43*(1-2), 193-234. doi: 10.1163/156854293X00296

Nottebohm, F. (2005). The neural basis of birdsong. *PLoS biology*, *3*(5), e164. doi: 10.1371/journal.pbio.0030164

Nottebohm, F., & Nottebohm, M. E. (1978a). Relationship between song repertoire and age in the canary, serinus canarius. *Zeitschrift für Tierpsychologie*, *46*(3), 298-305. doi: 10.1111/j.1439-0310.1978.tb01451.x

Nottebohm, F., & Nottebohm, M. E. (1978b). Relationship between song repertoire and age in the canary, serinus canarius. *Zeitschrift für Tierpsychologie*, *46*(3), 298-305. doi: 10.1111/j.1439-0310.1978.tb01451.x

Nottebohm, F., Nottebohm, M. E., Crane, L. A., & Wingfield, J. C. (1987). Seasonal changes in gonadal hormone levels of adult male canaries and their relation to song. *Behavioral and neural biology*, *47*(2), 197-211. doi: 10.1016/S0163-1047(87)90327-X

Nowicki, S., Hasselquist, D., Bensch, S., & Peters, S. (2000). Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1460), 2419-2424. doi: 10.1098/rspb.2000.1300

Nowicki, S., Peters, S., & Podos, J. (1998). Song learning, early nutrition and sexual selection in songbirds. *American Zoologist*, *38*(1), 179-190. doi: 10.1093/icb/38.1.179

Nowicki, S., Searcy, W., & Peters, S. (2002a). Brain development, song learning and mate choice in birds: a review and experimental test of the" nutritional stress hypothesis". *Journal of Comparative Physiology A*, *188*(11-12), 1003-1014. doi: 10.1007/s00359-002-0361-3

Nowicki, S., Searcy, W. A., Krueger, T., & Hughes, M. (2002). Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *Journal of Avian Biology*, *33*(3), 253-259. doi: 10.1034/j.1600-048X.2002.330307.x

Nowicki, S., Searcy, W. A., & Peters, S. (2002b). Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1503), 1949-1954. doi: 10.1098/rspb.2002.2124

Nowicki, S., Westneat, M., & Hoese, W. (n.d.). Birdsong: motor function and the evolution of communication. In *Seminars in neuroscience* (Vol. 4, p. 385-390). Elsevier. doi: 10.1016/1044-5765(92)90046-5

Nürnberger, F., Siebold, D., & Bergmann, H. (1989). Annual changes of learned behaviour-variation of song pattern in free-living chaffinches, *Fringilla coelebs*,

during the breeding season. *Bioacoustics*, *1*(4), 273-286. doi: 10.1080/09524622.1989.9753100

Oberweger, K., & Goller, F. (2001). The metabolic cost of birdsong production. *Journal of Experimental Biology*, *204*(19), 3379-3388.

Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E., & Langmore, N. E. (2014). Female song is widespread and ancestral in songbirds. *Nature Communications*, *5*, 3379. doi: 10.1038/ncomms4379

Odom, K. J., Omland, K. E., & Price, J. J. (2015). Differentiating the evolution of female song and male-female duets in the new world blackbirds: Can tropical natural history traits explain duet evolution? *Evolution*, *69*(3), 839-847. doi: 10.1111/evo.12588

Okanoya, K. (2004). Song syntax in bengalese finches: proximate and ultimate analyses. *Advances in the Study of Behavior*, *34*, 297-346. doi: 10.1016/S0065-3454(04)34008-8

Okanoya, K. (2013). *Finite-state song syntax in bengalese finches: sensorimotor evidence, developmental processes, and formal procedures for syntax extraction.* Cambridge, MA: MIT Press. doi: 10.7551/mitpress/9322.003.0016

Okanoya, K. (2017). Sexual communication and domestication may give rise to the signal complexity necessary for the emergence of language: An indication from songbird studies. *Psychonomic bulletin & review*, *24*(1), 106-110. doi: 10.3758/s13423-016-1165-8

Okanoya, K., & Yamaguchi, A. (1997). Adult bengalese finches (lonchura striata var. domestica) require real-time auditory feedback to produce normal song syntax. *Journal of neurobiology*, *33*(4), 343-356. doi: 10.1002/(SICI)1097-4695(199710)33:4<343::AID-NEU1>3.0.CO;2-A

Okubo, T. S., Mackevicius, E. L., Payne, H. L., Lynch, G. F., & Fee, M. S. (2015). Growth and splitting of neural sequences in songbird vocal development. *Nature*, *528*(7582), 352. doi: 10.1038/nature15741

O'Loghlen, A. L., & Rothstein, S. I. (1993). An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. *Animal Behaviour*, *46*(2), 293-304. doi: 10.1006/anbe.1993.1190

O'Loghlen, A. L., & Rothstein, S. I. (1995). Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behavioral Ecology and Sociobiology*, *36*(4), 251-259. doi: 10.1007/BF00165834

O'Loghlen, A. L., & Rothstein, S. I. (2002). Ecological effects on song learning: delayed development is widespread in wild populations of brown-headed cowbirds. *Animal Behaviour*, *63*(3), 475-486. doi: 10.1006/anbe.2001.1951

O-Shea, W., Serrano-Davies, E., & Quinn, J. L. (2017). Do personality and

innovativeness influence competitive ability? an experimental test in the great tit. *Behavioral Ecology*, *28*(6), 1435-1444. doi: 10.1093/beheco/arx104

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, *67*(4), 518-536. doi: 10.1046/j.1365-2656.1998.00215.x

Parker, K. A., Anderson, M. J., Jenkins, P. F., & Brunton, D. H. (2012). The effects of translocation-induced isolation and fragmentation on the cultural evolution of bird song. *Ecology Letters*, *15*(8), 778-785. doi: 10.1111/j.1461-0248.2012.01797.x

Pavlova, D. Z., Pinxten, R., & Eens, M. (2007). Seasonal singing patterns and individual consistency in song activity in female european starlings (sturnus vulgaris). *Behaviour*, *144*(6), 663-680. doi: 10.1163/156853907781347835

Payne, R. B., & Payne, L. L. (1997). Field observations, experimental design, and the time and place of learning bird songs. *Social influences on vocal development*, 57-84. doi: 10.1017/cbo9780511758843.005

Peek, F. W. (1972). An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (agelaius phoeniceus). *Animal Behaviour*, *20*(1), 112-118. doi: 10.1016/S0003-3472(72)80180-5

Perktaş, U., Peterson, A. T., & Dyer, D. (2017). Integrating morphology, phylogeography, and ecological niche modeling to explore population differentiation in north african common chaffinches. *Journal of Ornithology*, *158*(1), 1-13. doi: 10.1007/s10336-016-1361-3

Peters, S., Derryberry, E. P., & Nowicki, S. (2012). Songbirds learn songs least degraded by environmental transmission. *Biology letters*, *8*(5), 736-739. doi: 10.1098/rsbl.2012.0446

Peters, S., & Nowicki, S. (2017). Overproduction and attrition: the fates of songs memorized during song learning in songbirds. *Animal Behaviour*, *124*, 255-261. doi: 10.1016/j.anbehav.2016.09.019

Petrusková, T., Pišvejcová, I., Kinštová, A., Brinke, T., & Petrusek, A. (2016). Repertoire-based individual acoustic monitoring of a migratory passerine bird with complex song as an efficient tool for tracking territorial dynamics and annual return rates. *Methods in Ecology and Evolution*, *7*(3), 274-284. doi: 10.1111/2041-210X.12496

Pickstock, J. C., & Krebs, J. R. (1980). Neighbour-stranger song discrimination in the chaffinch (*Fringilla coelebs*). *Journal für Ornithologie*, *121*(1), 105-108. doi: 10.1007/BF01643260

Podos, J. (1996). Motor constraints on vocal development in a songbird. *Animal Behaviour*, *51*(5), 1061-1070. doi: 10.1006/anbe.1996.0107

Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations

in a songbird family (passeriformes: Emberizidae). *Evolution*, *51*(2), 537-551. doi: 10.2307/2411126

Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: the interface of evolution and mechanism. *Annu. Rev. Ecol. Evol. Syst.*, *35*, 55-87. doi: 10.1146/annurev.ecolsys.35.021103.105719

Podos, J., Moseley, D. L., Goodwin, S. E., McClure, J., Taft, B. N., Strauss, A. V., ... Lahti, D. C. (2016). A fine-scale, broadly applicable index of vocal performance: Frequency excursion. *Animal behaviour*, *116*, 203-212. doi: 10.1016/j.anbehav.2016.03.036

Podos, J., & Warren, P. S. (2007). The evolution of geographic variation in birdsong. *Advances in the Study of Behavior*, *37*, 403-458. doi: 10.1016/S0065-3454(07)37009-5

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Animal behaviour: elephants are capable of vocal learning. *Nature*, *434*(7032), 455.

Potvin, D. A., & Clegg, S. M. (2015). The relative roles of cultural drift and acoustic adaptation in shaping syllable repertoires of island bird populations change with time since colonization. *Evolution*, *69*(2), 368-380. doi: 10.1111/evo.12573

Prather, J. F., Peters, S., Nowicki, S., & Mooney, R. (2010). Persistent representation of juvenile experience in the adult songbird brain. *Journal of Neuroscience*, *30*(31), 10586-10598. doi: 10.1523/JNEUROSCI.6042-09.2010

Price, J. J. (2015). Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. *Frontiers in Ecology and Evolution*, *3*(40). doi: 10.3389/fevo.2015.00040

Price, J. J., Lanyon, S. M., & Omland, K. E. (2009). Losses of female song with changes from tropical to temperate breeding in the new world blackbirds. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb.2008.1626. doi: 10.1098/rspb.2008.1626

Price, P. H. (1979). Developmental determinants of structure in zebra finch song. *journal of comparative and physiological psychology*, *93*(2), 260. doi: 10.1037/h0077553

Rando, J. C., Alcover, J. A., & Illera, J. C. (2010). Disentangling ancient interactions: a new extinct passerine provides insights on character displacement among extinct and extant island finches. *PLoS One*, *5*(9), e12956. doi: 10.1371/journal.pone.0012956

Ravignani, A. (2017). Visualizing and interpreting rhythmic patterns using phase space plots. *Music Perception: An Interdisciplinary Journal*, *34*(5), 557-568. doi: 10.1525/MP.2017.34.5.557

Read, A. F., & Weary, D. M. (1992). The evolution of bird song: comparative

analyses. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *338*(1284), 165-187. doi: 10.1098/rstb.1992.0137

Reed, T. M. (1982). Interspecific territoriality in the chaffinch and great tit on islands and the mainland of scotland: playback and removal experiments. *Animal behaviour*, *30*(1), 171-181. doi: 10.1016/S0003-3472(82)80252-2

Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in cognitive sciences*, *15*(2), 68-76. doi: 10.1016/j.tics.2010.12.002

Riebel, K. (2003). The "mute" sex revisited: vocal production and perception learning in female songbirds. *Advances in the Study of Behavior*, *33*(4). doi: 10.1016/S0065-3454(03)33002-5

Riebel, K. (2016). Understanding sex differences in form and function of bird song: The importance of studying song learning processes. *Frontiers in Ecology and Evolution*, *4*(62). doi: 10.3389/fevo.2016.00062

Riebel, K., Hall, M. L., & Langmore, N. E. (2005). Female songbirds still struggling to be heard. *Trends in Ecology & Evolution*, *20*(8), 419-420. doi: 10.1016/j.tree.2005.04.024

Riebel, K., Lachlan, R. F., & Slater, P. J. (2015). Learning and cultural transmission in chaffinch song. In *Advances in the study of behavior* (Vol. 47, p. 181-227). Elsevier. doi: 10.1016/bs.asb.2015.01.001

Riebel, K., Odom, K. J., Langmore, N. E., & Hall, M. L. (2019). New insights from female bird song: towards an integrated approach to studying male and female communication roles. *Biology letters*, *15*(4), 20190059. doi: 10.1098/rsbl.2019.0059

Riebel, K., & Slater, P. J. (1998a). Male chaffinches (fringilla coelebs) can copy calls from a tape tutor. *Journal für Ornithologie*, *139*(3), 353–355.

Riebel, K., & Slater, P. J. (1998b). Testing female chaffinch song preferences by operant conditioning. *Animal Behaviour*, *56*(6), 1443-1453. doi: 10.1006/anbe.1998.0933

Riebel, K., & Slater, P. J. (1999a). Do male chaffinches *Fringilla coelebs* copy song sequencing and bout length from their tutors? *Ibis*, *141*(4), 680-683. doi: 10.1111/j.1474-919x.1999.tb07376.x

Riebel, K., & Slater, P. J. (1999b). Song type switching in the chaffinch, *Fringilla coelebs*: timing or counting? *Animal behaviour*, *57*(3), 655-661. doi: 10.1006/anbe.1998.0984

Rivera-Gutierrez, H. F., Pinxten, R., & Eens, M. (2015). Songbirds never forget: long-lasting behavioural change triggered by a single playback event. *Behaviour*, *152*(9), 1277-1290. doi: 10.1163/1568539X-00003278

Roper, M. M., Harmer, A. M., & Brunton, D. H. (2018). Developmental changes in song production in free-living male and female new zealand bellbirds. *Animal Behaviour*, *140*, 57-71. doi: 10.1016/j.anbehav.2018.04.003

Saar, S., & Mitra, P. P. (2008). A technique for characterizing the development of rhythms in bird song. *PLoS One*, *3*(1), e1461.

Sangster, G., Rodríguez-Godoy, F., Roselaar, C., Robb, M. S., & Luksenburg, J. A. (2016). Integrative taxonomy reveals europe's rarest songbird species, the gran canaria blue chaffinch fringilla polatzeki. *Journal of Avian Biology*, *47*(2), 159-166. doi: 10.1111/jav.00825

Sasahara, K., Tchernichovski, O., Takahasi, M., Suzuki, K., & Okanoya, K. (2015). A rhythm landscape approach to the developmental dynamics of birdsong. *Journal of the Royal Society Interface*, *12*(112), 20150802. doi: 10.1098/rsif.2015.0802

Scharff, C., & Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. *Journal of Neuroscience*, *11*(9), 2896-2913.

Schmidt, K. L., MacDougall-Shackleton, E. A., Kubli, S. P., & MacDougall-Shackleton, S. A. (2014). *Developmental stress, condition, and birdsong: a case study in song sparrows* (Vol. 54) (No. 4). The Society for Integrative and Comparative Biology. doi: 10.1093/icb/icu090

Searcy, W. A. (1992a). Measuring responses of female birds to male song. In *Playback and studies of animal communication* (p. 175-189). Springer. doi: 10.1007/978-1-4757-6203-7_12

Searcy, W. A. (1992b). Song repertoire and mate choice in birds. *American Zoologist*, *32*(1), 71-80. doi: 10.1093/icb/32.1.71

Searcy, W. A., Balaban, E., Canady, R. A., Clark, S. J., Runfeldt, S., & Williams, H. (1981). Responsiveness of male swamp sparrows to temporal organization of song. *The Auk*, 613-615. doi: 10.1093/auk/98.3.613

Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour*, *78*(6), 1281-1292. doi: 10.1016/j.anbehav.2009.08.011

Searcy, W. A., Marler, P., & Peters, S. S. (1985). Songs of isolation-reared sparrows function in communication, but are significantly less effective than learned songs. *Behavioral Ecology and Sociobiology*, *17*(3), 223-229. doi: 10.1007/BF00300140

Searcy, W. A., & Yasukawa, K. (2014). *Polygyny and sexual selection in red-winged blackbirds*. Princeton University Press. doi: 10.2307/2265684

Seddon, N., & Tobias, J. A. (2005). Duets defend mates in a suboscine passerine, the warbling antbird (hypocnemis cantator). *Behavioral Ecology*, *17*(1), 73-83. doi: 10.1093/beheco/ari096

Sheldon, B., & Burke, T. (1994). Copulation behavior and paternity in the chaffinch. *Behavioral Ecology and Sociobiology*, *34*(2), 149–156. doi: 10.1007/BF00164185

Slabbekoorn, H., & Smith, T. B. (2002a). Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1420), 493-503. doi: 10.1098/rstb.2001.1056

Slabbekoorn, H., & Smith, T. B. (2002b). Habitat-dependent song divergence in the little greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution*, *56*(9), 1849-1858. doi: 10.1111/j.0014-3820.2002.tb00199.x

Slagsvold, T. (1977). Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scandinavica*, 197-222. doi: 10.2307/3676105

Slater, P. J. (1981). Chaffinch song repertoires: observations, experiments and a discussion of their significance. *Ethology*, *56*(1), 1-24. doi: 10.1111/j.1439-0310.1981.tb01280.x

Slater, P. J. (1983). Chaffinch imitates canary song elements and aspects of organization. *The Auk*, *100*(2), 493-495. doi: 10.1093/auk/100.2.493

Slater, P. J. (1989). Bird song learning: causes and consequences. *Ethology Ecology & Evolution*, *1*(1), 19-46. doi: 10.1080/08927014.1989.9525529

Slater, P. J., & Catchpole, C. K. (1990). Responses of the two chaffinch species on tenerife (fringilla teydea and f. coelebs tintillon) to playback of the song of their own and the other species. *Behaviour*, *115*(3), 143-152. doi: 10.1163/156853990X00545

Slater, P. J., Clements, F., & Goodfellow, D. (1984). Local and regional variations in chaffinch song and the question of dialects. *Behaviour*, 76-97.

Slater, P. J., & Ince, S. (1979). Cultural evolution in chaffinch song. *Behaviour*, *71*(1), 146-166. doi: 10.1163/156853979X00142

Slater, P. J., Ince, S., & Colgan, P. (1980). Chaffinch song types: their frequencies in the population and distribution between repertoires of different individuals. *Behaviour*, *75*(3), 207-218.

Slater, P. J., & Mann, N. I. (2004). Why do the females of many bird species sing in the tropics? *Journal of Avian Biology*, *35*(4), 289-294. doi: 10.1111/j.0908-8857.2004.03392.x

Sonnenschein, E., & Reyer, H.-U. (1983). Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (laniarius funebris) 1. *Zeitschrift für Tierpsychologie*, *63*(2-3), 112-140. doi: 10.1111/j.1439-0310.1983.tb00083.x

Spencer, K., Buchanan, K., Goldsmith, A., & Catchpole, C. K. (2003). Song

as an honest signal of developmental stress in the zebra finch (taeniopygia guttata). *Hormones and Behavior*, *44*(2), 132-139. doi: 10.1016/S0018-506X(03)00124-7

Spencer, K., Wimpenny, J., Buchanan, K., Lovell, P., Goldsmith, A., & Catchpole, C. K. (2005). Developmental stress affects the attractiveness of male song and female choice in the zebra finch (taeniopygia guttata). *Behavioral Ecology and Sociobiology*, *58*(4), 423-428. doi: 10.1007/s00265-005-0927-5

Spierings, M. J., & ten Cate, C. (2016). Zebra finches as a model species to understand the roots of rhythm. *Frontiers in neuroscience*, *10*, 345. doi: 10.3389/fnins.2016.00345

Stoddard, P. K., Beecher, M. D., Horning, C. L., & Willis, M. S. (1990). Strong neighbor-stranger discrimination in song sparrows. *The Condor*, *92*(4), 1051-1056.

Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *The Journal of the Acoustical Society of America*, *119*(3), 1849-1866.

Suárez, N. M., Betancor, E., Klassert, T. E., Almeida, T., Hernández, M., & Pestano, J. J. (2009). Phylogeography and genetic structure of the canarian common chaffinch (*Fringilla coelebs*) inferred with mtdna and microsatellite loci. *Molecular phylogenetics and evolution*, *53*(2), 556-564. doi: 10.1016/j.ympev.2009.07.018

Svensson, B. W. (1978). Clutch dimensions and aspects of the breeding strategy of the chaffinch fringilla coelebs in northern europe: a study based on egg collections. *Ornis Scandinavica*, 66–83.

Svensson, L. (2015). A new north african subspecies of common chaffinch *Fringilla coelebs*. *Bull. Br. Orn. Club*, *135*, 69-76.

Takahasi, M., & Okanoya, K. (2010). Song learning in wild and domesticated strains of white-rumped munia, lonchura striata, compared by cross-fostering procedures: domestication increases song variability by decreasing strain-specific bias. *Ethology*, *116*(5), 396-405. doi: 10.1111/j.1439-0310.2010.01761.x

Tchernichovski, O., Lints, T., Derégnaucourt, S., Cimenser, A., & Mitra, P. P. (2004). Studying the song development process: rationale and methods. *Annals of the New York academy of sciences*, *1016*(1), 348-363. doi: 10.1196/annals.1298.031

Tchernichovski, O., Lints, T., Mitra, P. P., & Nottebohm, F. (1999). Vocal imitation in zebra finches is inversely related to model abundance. *Proceedings of the National Academy of Sciences*, *96*(22), 12901-12904. doi: 10.1073/pnas.96.22.12901

Tchernichovski, O., Mitra, P. P., Lints, T., & Nottebohm, F. (2001). Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science*, *291*(5513), 2564-2569. doi: 10.1126/science.1058522

Team, R. (2015). Rstudio: integrated development for r. *RStudio, Inc., Boston, MA*, *42*, 14. Retrieved from `www.rstudio.com`

Templeton, C. N., Burt, J. M., Campbell, S. E., Lent, K., Brenowitz, E. A., & Beecher, M. D. (2012). Immediate and long-term effects of testosterone on song plasticity and learning in juvenile song sparrows. *Behavioural processes*, *90*(2), 254-260. doi: 10.1016/j.beproc.2012.02.002

ten Cate, C., Spierings, M., Hubert, J., & Honing, H. (2016). Can birds perceive rhythmic patterns? a review and experiments on a songbird and a parrot species. *Frontiers in psychology*, *7*, 730. doi: 10.3389/fpsyg.2016.00730

Thielcke, G. (1973). On the origin of divergence of learned signals (songs) in isolated populations. *Ibis*, *115*(4), 511-516. doi: 10.1111/j.1474-919X.1973.tb01989.x

Thielcke, G., & Krome, M. (1991). Chaffinches *Fringilla coelebs* do not learn song during autumn and early winter. *Bioacoustics*, *3*(3), 207–212. doi: 10.1080/09524622.1991.9753180

Thomas, R. J. (1999). Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Animal Behaviour*, *57*(2), 277-284. doi: 10.1006/anbe.1998.0956

Thomas, R. J. (2002). The costs of singing in nightingales. *Animal Behaviour*, *63*(5), 959-966. doi: 10.1006/anbe.2001.1969

Thorpe, W. H. (1954). The process of song-learning in the chaffinch as studied by means of the sound spectrograph. *Nature*, *173*(4402), 465. doi: 10.1038/173465a0

Thorpe, W. H. (1955). Comments on 'the bird fancyer's delight': Together with notes on imitation in the sub-song of the chaffinch. *Ibis*, *97*(2), 247-251. doi: 10.1111/j.1474-919X.1955.tb01911.x

Thorpe, W. H. (1958a). Further studies on the process of song learning in the chaffinch (*Fringilla coelebs* gengleri). *Nature*, *182*(4635), 554. doi: 10.1038/182554a0

Thorpe, W. H. (1958b). The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis*, *100*(4), 535-570. doi: 10.1111/j.1474-919X.1958.tb07960.x

Thorpe, W. H. (1961). Bird-song: the biology of vocal communication and expression in birds.

Thorpe, W. H., & Pilcher, P. (1958). The nature and characteristics of subsong. *British birds*, *51*(12), 509-14.

Tobias, J., Gamarra-Toledo, V., García-Olaechea, D., Pulgarin, P., & Seddon, N. (2011). Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *Journal of evolutionary biology*, *24*(10), 2118-2138. doi: 10.1111/j.1420-9101.2011.02345.x

Todt, D., Hultsch, H., & Heike, D. (1979). Conditions affecting song acquisition in nightingales (luscinia megarhynchos l.). *Zeitschrift für Tierpsychologie*, *51*(1), 23-35. doi: 10.1111/j.1439-0310.1979.tb00668.x

Voigt, C., Leitner, S., & Gahr, M. (2001). Seasonal changes in the song pattern of the non-domesticated island canary (serinus canaria) a field study. *Behaviour*, *138*(7), 885–904.

Warburg, G. (1941). Song of female chaffinch. *Brit. Birds*, *34*, 261.

Watson, M. (1969). Significance of antiphonal song in the eastern whipbird, psophodes olivaceus. *Behaviour*, *35*(1-2), 157-178. doi: 10.1163/156853970X00187

Webb, W. H., Brunton, D. H., Aguirre, J. D., Thomas, D. B., Valcu, M., & Dale, J. (2016). Female song occurs in songbirds with more elaborate female coloration and reduced sexual dichromatism. *Frontiers in Ecology and Evolution*, *4*(22). doi: 10.3389/fevo.2016.00022

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences*, *110*(38), 15307-15312. doi: 10.1073/pnas.1306309110

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: ecology, evolution, and conservation.* Oxford University Press.

Wickler, W., & Seibt, U. (1980). Vocal dueting and the pair bond: Ii. unisono dueting in the african forest weaver, symplectes bicolor. *Zeitschrift für Tierpsychologie*, *52*(3), 217-226. doi: 10.1111/j.1439-0310.1980.tb00713.x

Williams, J., & Slater, P. J. (1993). Does chaffinch *Fringilla coelebs* song vary with the habitat in which it is sung? *Ibis*, *135*(2), 202-208. doi: 10.1111/j.1474-919X.1993.tb02833.x

Woodgate, J. L., Bennett, A. T., Leitner, S., Catchpole, C. K., & Buchanan, K. L. (2010). Developmental stress and female mate choice behaviour in the zebra finch. *Animal Behaviour*, *79*(6), 1381-1390. doi: 10.1016/j.anbehav.2010.03.018

Zann, R. A. (1996). *The zebra finch: a synthesis of field and laboratory studies* (Vol. 5). Oxford University Press. doi: 10.1086/420003

Zuccon, D., Prŷs-Jones, R., Rasmussen, P. C., & Ericson, P. G. (2012). The phylogenetic relationships and generic limits of finches (fringillidae). *Molecular Phylogenetics and Evolution*, *62*(2), 581–596.